

PLANT-FOSSIL TAPHONOMY, LATE PENNSYLVANIAN KINNEY QUARRY, NEW MEXICO, USA

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Abstract—Large numbers of plant fossils have been collected from the early Late Pennsylvanian (Missourian/Kasimovian) age Kinney Brick Company Quarry, southeast of Albuquerque, New Mexico. This location was the focus of a multi-disciplinary study, published in 1992 by the New Mexico Bureau of Mines and Mineral Resources as a collection of papers, and has been the source of animal and plant fossils published in numerous additional papers. In 2014, geologists from the Bergakademie in Freiberg, Germany and the New Mexico Museum of Natural History and Science (NMMNHS) in Albuquerque carried out a controlled excavation through the fossiliferous shales exposed in the quarry floor. The fossil-bearing beds record a marine to brackish or nonmarine transition in a shallowing-upward sedimentary sequence, likely that of a sheltered embayment into which a delta prograded. Changes in the sedimentary environment were accompanied by changes in composition and relative taxonomic abundances of the vertebrate, invertebrate, and plant-fossil assemblages, as well as changes in the size of plant fragments from small to large upward in the fill sequence.

In this study, we report a detailed investigation of the Kinney Quarry plant fossils held by the NMMNHS, many collected during the 2014 controlled excavation. The collections made in the excavation, and their distinctive and diagnostic lithological attributes, also served as a guide by which to sort stratigraphically the large plant collections from Kinney held by the National Museum of Natural History (NMNH). The latter collections were made at several different places, and from several different levels in the fossiliferous shales preserved in the quarry, primarily in May of 1967 and 1969. From the analyses of the NMNH and NMMNHS collections, the following generalities emerge: (1) Plant fossils occur in a 2.5 m-thick siltstone that changes in character upsection. All fossil-plant assemblages are allochthonous to varying degrees, diminishing upward in the fill sequence. (2) The flora, viewed as a whole, is a mixture of wetland and drought-tolerant taxa, which, based on the form of preservation, lived in close proximity to one another in the source area of the surrounding ancient coastline. (3) There are changes in the plant-fossil composition and preservation from the lower to the upper beds in the siliciclastic fill exposed in the quarry: (a) Wetland taxa dominate the farthest offshore deposits; xeromorphic, presumed more drought-tolerant taxa, increase in relative abundance in the upper beds. (b) Plant-fragment mean-size increases from the lowermost to the uppermost bed analyzed, which is congruent with increasing proximity to the paleo-shoreline. (4) The NMMNHS and NMNH collections, made in different areas of the quarry, are similar compositionally when sorted by stratigraphic collecting level. (5) The detailed, bed-scale excavations permitted the revitalization of museum collections made earlier and without reference to bed-scale stratigraphic position, thus permitting a more complete interpretation of fine-scale environmental and floral changes that otherwise could not be determined from the older collections alone.

INTRODUCTION

Located in the Manzanita Mountains of central New Mexico, the Kinney Brick Quarry is a clay pit actively mined for the making of bricks at the Kinney Brick Company plant in Albuquerque, New Mexico. The strata mined are Upper Pennsylvanian (Missourian) estuarine deposits of the Tinajas Member of the Atrasado Formation. These strata yield a diverse and exceptionally preserved biota that identifies the Kinney fossil deposit as a remarkable Lagerstätte (Zidek, 1992; Lucas et al., 2011). The Kinney Quarry has produced a well preserved fossil flora that is intermixed intimately with a fauna of both invertebrates and vertebrates. The paleo-location of the site was in western Pangea at approximately 10 degrees North latitude (Boucot et al., 2013, map 13). The flora has been described both piecemeal and in two large floristic syntheses, and is reasonably well known (Mamay and Mapes, 1992; DiMichele et al., 2013). It is a “mixed” flora of plants thought to be typical

of seasonally dry climatic conditions, tolerant of some degree of drought (*Sphenopteris germanica*, walchian conifers, the coniferophyte *Dicranophyllum* among others), as well as a subset of typical Late Pennsylvanian wetland species, most notably the pteridosperm *Neuropteris ovata*, marattialeean ferns, calamitaleean sphenopsids, and rare sigillarian lycopsids.

The present study is based on two suites of plant fossils. The principal collection, around which the study is organized, is held by the New Mexico Museum of Natural History and Science (NMMNHS). Although the collections were made over many years, the majority analyzed for this study were made in 2014, as part of a controlled excavation. The other collection is held by the National Museum of Natural History (NMNH or USNM), part of the Smithsonian Institution. The NMNH collections were made primarily under the supervision of U. S. Geological Survey (USGS) paleobotanist Sergius Mamay, in 1967 and 1969. An earlier, small collection was made by Charles B. Read, also of the U.S. Geological Survey.

Several published studies describe the fossils from and the geology of the strata exposed at Kinney. The most comprehensive is a volume edited by Zidek (1992), including papers that examine the sedimentology, stratigraphy, the likely paleoclimate, and various groups of fossil plants, invertebrates, and vertebrates from the quarry. Specific paleobotanical papers based entirely on the Kinney flora, or specific plant taxa from the site, include macroflora floristic studies (Mamay and Mapes, 1992; DiMichele et al., 2013), a palynological investigation (Willard, 1992), and descriptions of *Dicranophyllum readii* (Mamay, 1981), *Charliea manzanitana* (Mamay, 1990), and *Sphenopteridium manzanitanum* (Mamay, 1992). Eggs of some aquatic organism, possibly fish, have been found attached to leaves (Mamay, 1994), and insect and pathogen damage associated with the Kinney flora (Donovan and Lucas, this volume) also have been described.

The present study aims to describe the taphonomic aspects of the Kinney fossil flora, based on comparisons of the NMMNHS and NMNH plant-fossil collections. Those of the NMMNHS are of particular interest because, as noted, a subset of them was made in the course of a controlled excavation that revealed distinct lithological and plant-fossil compositional changes through the thickness of the main fossiliferous beds. The NMNH collections were made without reference to bed positions. They were sorted, for this study, into likely source beds based on lithological and non-plant fossil characteristics, as established by the NMMNHS controlled excavation. This taphonomic study provides greater documentation of the vegetation surrounding the site and the nature of changes in that vegetation through the interval of accumulation than was possible previously. The study demonstrates how, when collecting plant fossils, attention to geological features at the outcrop scale can reveal unexpected paleoenvironmental patterns. Also demonstrated is the enhanced value gained from older museum collections, originally obtained for one set of research objectives, when linked to modern field observations and repurposed to address new and different research problems.

GEOLOGY OF THE KINNEY QUARRY

The Kinney Brick Company Quarry is located in the Manzanita Mountains, approximately 12 km south of Tijeras, in Bernalillo County, New Mexico, in the Sedillo 7 1/2' Quadrangle (section 18, T9N, R6E). Fusulinid and conodont biostratigraphy establishes the age of the strata exposed at the quarry as Missourian, thus within the Kasimovian stage of the Late Pennsylvanian (Lucas et al., 2011), approximately 305 MyBP. In their analysis of the flora, DiMichele et al. (2013) noted that the flora shared many taxa with European floras of late Stephanian age, typical of the Autunian and lower Rotliegend in France and Germany, which led some of the authors to conclude that the Kinney Quarry deposit must be of this younger age.

The deposition of the strata of interest, a 2.5 m thick sequence of claystones and siltstones (Fig. 1) that contain plant and animal fossils, took place in a muddy, restricted coastal embayment, becoming ever closer to the coastline as it was filled-in by siliciclastic sediment (Archer and Clark, 1992; Kues and Lucas, 1992; Feldman et al., 1992; Lorenz et al., 1992; Schneider et al., 2021, this volume). The prevailing climate is considered to have been seasonal and monsoonal (e.g. Tabor and Poulsen, 2008; Schneider et al., 2021, this volume). Initially a carbonate lagoon, subsequent sediment delivery has been interpreted to result from the progradation of a delta front into the embayment (Archer and Clark, 1992; Lorenz et al., 1992). The full deposit, much of which lies above the plant-fossil beds, has characteristics of a constructional, river-dominated delta, in its shallowing-upward character, terminating in fluvial sandstone beds (Schneider et al., 2021, this volume). The lower six beds of the section contain most of the plant fossils. Of these,

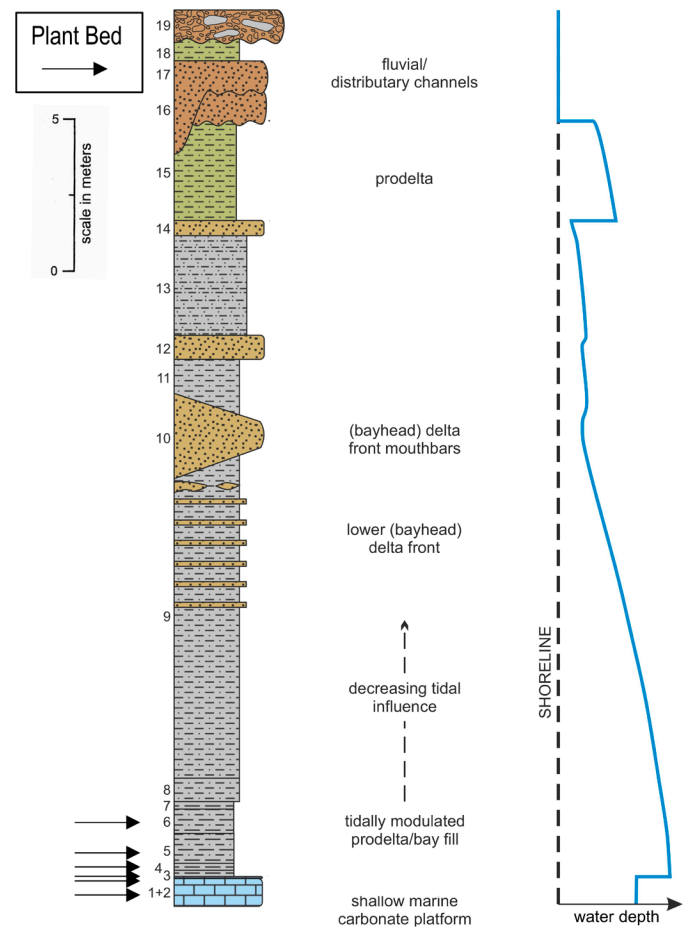


FIGURE 1. Sequence of lithofacies through the lower beds of the Kinney Quarry geologic succession. Beds 1-6, from which plant fossils were collected, are numbered as described in the text. Stratigraphic column, sedimentological interpretations, and water-depth estimate from Schneider et al. (2021, this volume) with permission.

Bed 3 through Bed 5 have fine, millimeter-scale laminations, within which the bedding is graded, mainly coarsening upward. These laminations, interpreted by some authors as of strictly tidal origin (Archer and Clark, 1992), are now considered to reflect seasonal river floods with some tidal modulation, under a seasonally dry climatic regime (Schneider et al., 2021, this volume). Furthermore, these finely laminated shales show almost no evidence of bioturbation, and lack infaunal trace fossils and benthic organisms, leading to the conclusion that the bottom waters were oxygen depleted. Oxygen depletion may have resulted from poor mixing and restricted circulation in the embayment and from high productivity.

The plant-bearing lower beds likely accumulated during a period of greater than 1000 years. Bed 5 and Bed 6, a 1.9 m thick succession at the top of the laminated siltstones, contain concentrations of large valves of the clam *Dunbarella* (Kues (1992b)). Those siltstones are composed of about 1000 laminae, with an average thickness of 2 mm each. Given that each lamina was produced during an annual flood season, these two beds alone would account for 1000 years of deposition. Thus, the entire suite of Bed 1 through Bed 6 might account for more than twice that interval of time.

As Lorenz et al. (1992) argued, the geological section exposed in the Kinney Quarry represents a migration of the shoreline over the quarry area (Williams and Lucas, 2013; Schneider et al., 2021, this volume). From the base, the section begins with strata

formed in a relatively shallow marine environment, represented by a micritic bioclastic limestone (Bed 1) and a silty micritic limestone (Bed 2). A deepening of the embayment, possibly due to tectonic causes, was followed by a shallowing-upward sequence of finely laminated calcareous siltstone (Bed 3). Above Bed 3 the section coarsens upward to laminated siltstone (Beds 4-5), interpreted as prodeltaic muds (Kues and Lucas, 1992; Schneider et al., 2021, this volume). Seasonal river floods continued to transport clastics into the prodelta area. There is little evidence of deep scour of the laminated siltstone beds, which suggests that a major river did not flow directly into the area of the deposit during the time the lower, plant-fossil beds were being deposited. The uppermost bed bearing significant plant-fossils (Bed 6) differs from the underlying beds, and is a relatively thick mudstone that is somewhat massive, and not finely laminated. Coarse-grained fluvial sediments erosively truncate the upper layers of fossiliferous mudstone.

Vertebrate remains, particularly fish, are most commonly encountered in the lowermost, shaly limestones and calcareous siltstone units (Bed 3), and are rare in the overlying siltstone portions of the sequence. Conversely, plant remains are rare and generally highly fragmentary in the lower parts of the embayment fill (Beds 2 and 3) but become proportionally more abundant and of larger size upward (Beds 4 and 5). Invertebrates typical of brackish-to-fresh-water salinities are generally relatively rare in the lowermost siltstone beds and become more abundant upward within the fill, also increasing in size. They are represented most conspicuously by the bivalve *Dunbarella* (Kues, 1992).

Based on the overall sequence, and on the nature of the sediments, water depths are inferred to have been perhaps as much as 15 m. The taxonomic composition and upward

diminishment of the fish fauna, and the increasingly abundant *Dunbarella* upward, indicate that initial largely marine to brackish salinities were replaced by increasingly fresh-water conditions in the upper portions of the deposit (Williams and Lucas, 2013).

COLLECTIONS

The Kinney Quarry collections analyzed in this study come from three main parts of the quarry, made at different times, as the quarrying operation progressed (Fig. 2). The oldest collections, made in the 1960s by the USGS under the supervision of Sergius H. Mamay, come from near the present quarry entrance (UTM 377996E, 3874046N). Later, primarily in the 1990s, collections were made from areas farther into the quarry by Philip Huber (UTM 377915E, 3873903N), then a volunteer at the NMMNHS. Lastly, the controlled excavation, described below, was carried out in 2014, still farther into the quarry (UTM 377854E 3873854N), but closer to the Huber collection area than that of Mamay.

This study was initiated as a consequence of the controlled excavation carried out between April 28 and May 7, 2014 by a team from the New Mexico Museum of Natural History and Science, Albuquerque, NM, USA, and the Technical University Bergakademie, Freiberg, Germany. The excavation team was led by coauthors Lucas and Schneider. The excavation focused on shales that are the primary fossiliferous interval exposed near the floor at the Kinney Quarry.

The beds in the excavation were numbered sequentially from the bottom upward, Bed 1 to Bed 6. Most of the fossils came from Bed 2 to Bed 5 (Figs. 1, 3). Some of the beds were subdivided into subunits (Schneider et al., 2021, this volume, Table 1).

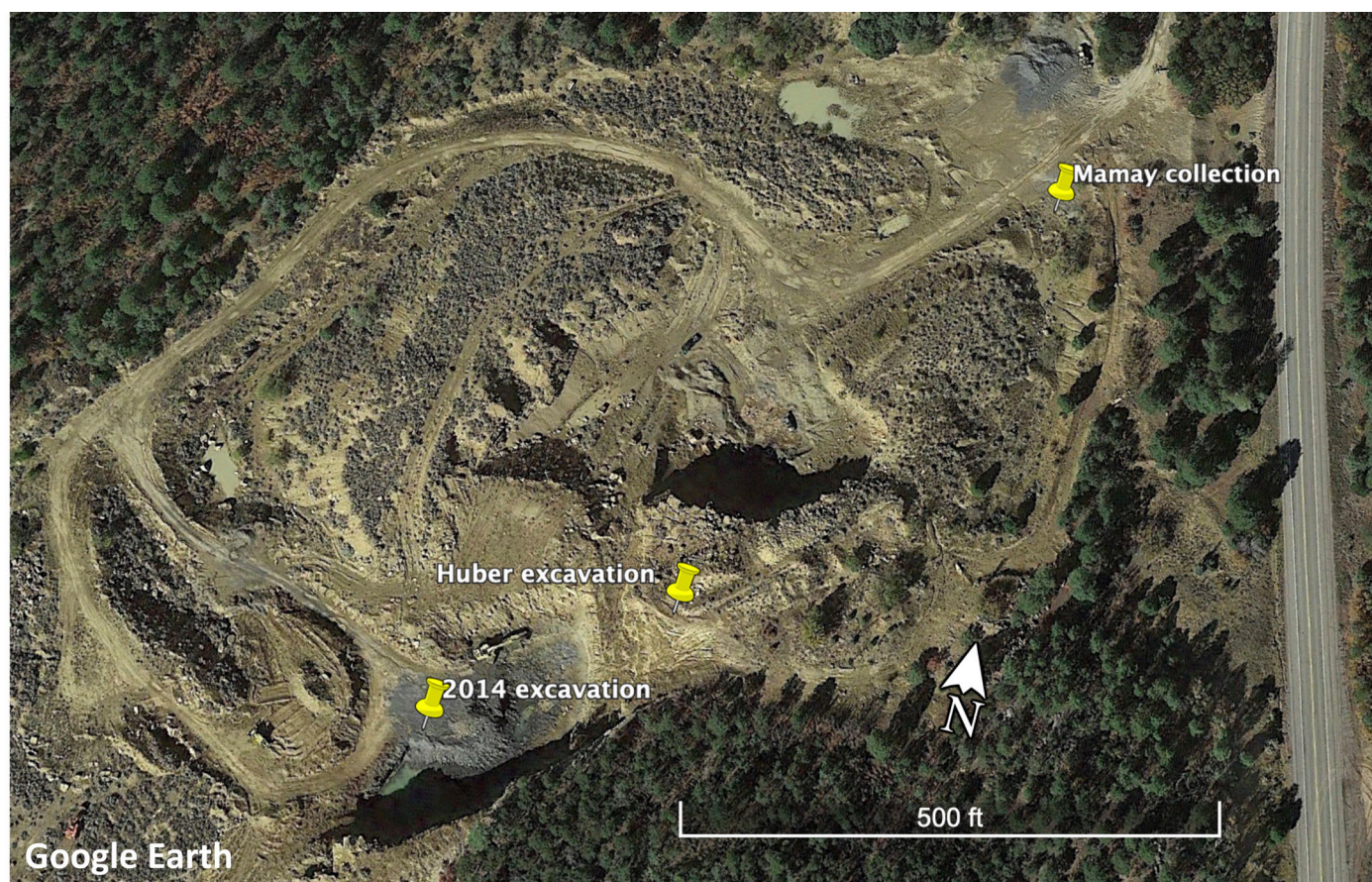


FIGURE 2. Aerial photograph of the Kinney quarry showing the locations of collections made by the USGS (Mamay), the NMMNHS (Huber), and the combined American-German team in 2014. Image courtesy of Google Earth.

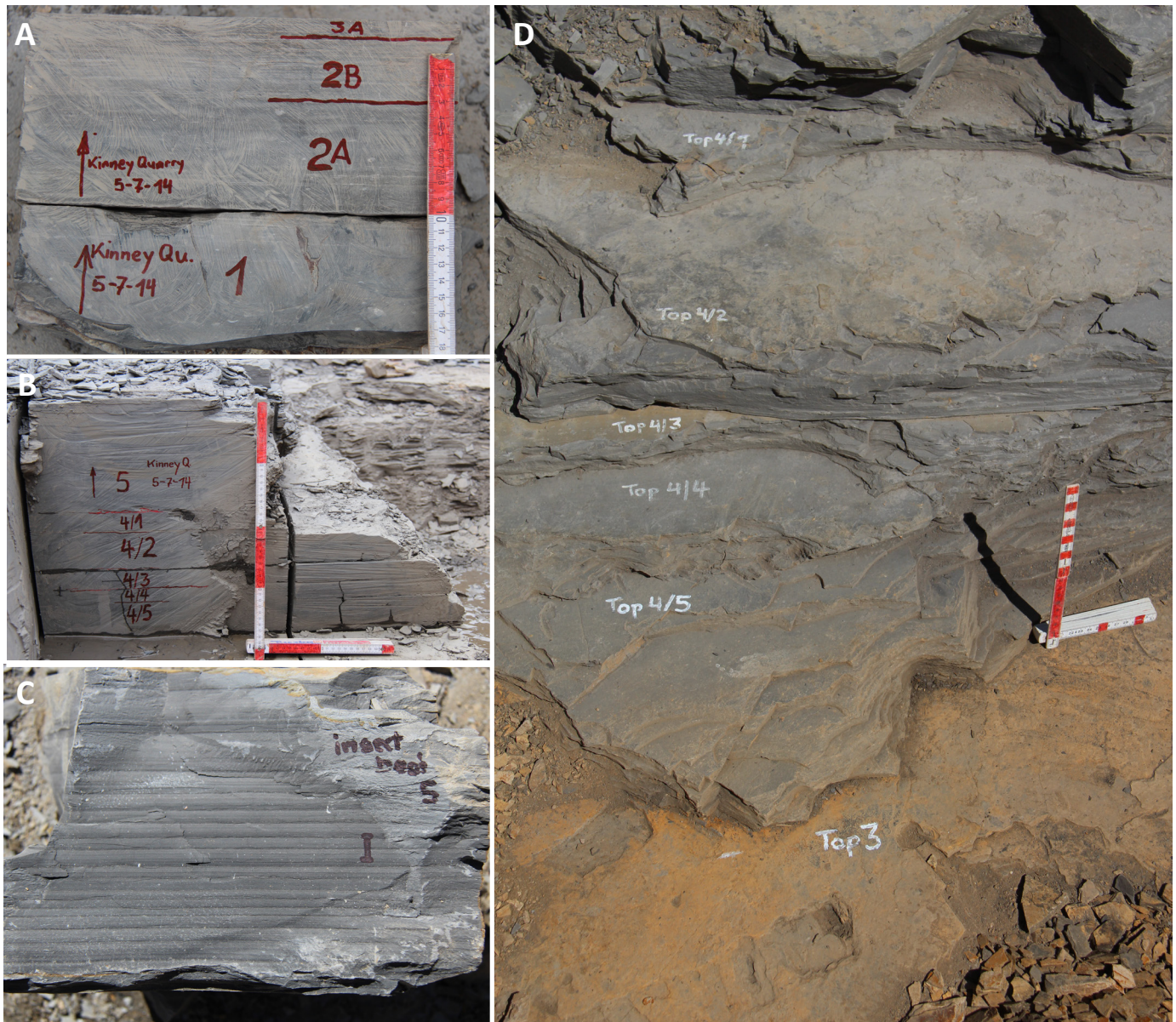


FIGURE 3. Fossiliferous beds in the Kinney controlled excavation, May 2014. A. Lower part of excavation. Beds 1, 2, and 3. Note that Bed 1 is a limestone. It transitions to a silty micritic limestone (Bed 2), and laminated, calcareous siltstone (Bed 3). B. Upper part of excavation. Beds 4 and 5. C. Detail of Bed 5 showing regular lamination. D. Transition from Bed 3 to Bed 4. Bed 3 is particularly noteworthy for the abundance of iron-staining that typifies even freshly excavated blocks. Note the sparseness of organic matter; after close examination, only comminuted debris is visible on the bedding surfaces.

The Controlled Excavation

In conducting the controlled excavation (Fig. 4), an area of the quarry floor was cleared to the level of Bed 5. The lower ½ of Bed 5 was excavated. Thus, the majority of Bed 5 specimens are not referenced to a particular sampling grid, although they are strictly controlled for bed. On the upper surface of Bed 4, a grid of 6 m² was marked off in a rectangular array, 3 m x 2 m. These are referenced as Excavation (E) 1-3, and Section (S) 1 or 2. Each square meter was excavated downward through Bed 4 and Bed 3. Bed 2 was collected from an area of 0.9 m x 0.5 m, through a 10 cm thickness only, without strict reference to grid. The total thickness of the plant-fossil bearing portion of the excavation was 2.5 m.

Details of the excavation and sedimentology of the various beds are described in the accompanying paper in this volume by Schneider et al. (2021, this volume). The plant fossils from the

various beds are illustrated in Donovan et al. (2021, this volume) and Looy et al. (2021, this volume). A brief summary of the characteristics of the beds is given here.

Bed 1 is a gray marine limestone (Fig. 1, Bed 1; Fig. 3), ≥1m thickness. It includes a restricted-marine fauna (Kues, 1992a; Kues and Lucas, 1992) dominated by brachiopods, but contains some scraps of plant material, intermixed with the marine invertebrate fossils.

Bed 2 is an 11 cm thick, micritic limestone. It contains a few marine invertebrates and a sparse assemblage of plant remains, which are generally highly fragmentary (Fig. 1, Bed 2; Fig. 3).

Bed 3 is a finely laminated bituminous limestone to calcareous siltstone, as much as 16 cm thick (Fig. 1, Bed 3; Fig. 3), gray to buff in color and with distinctive iron oxide (Liesegang) banding. It splits into large, thin sheets. This bed produces the bulk of the Kinney fossil fish assemblage (Williams

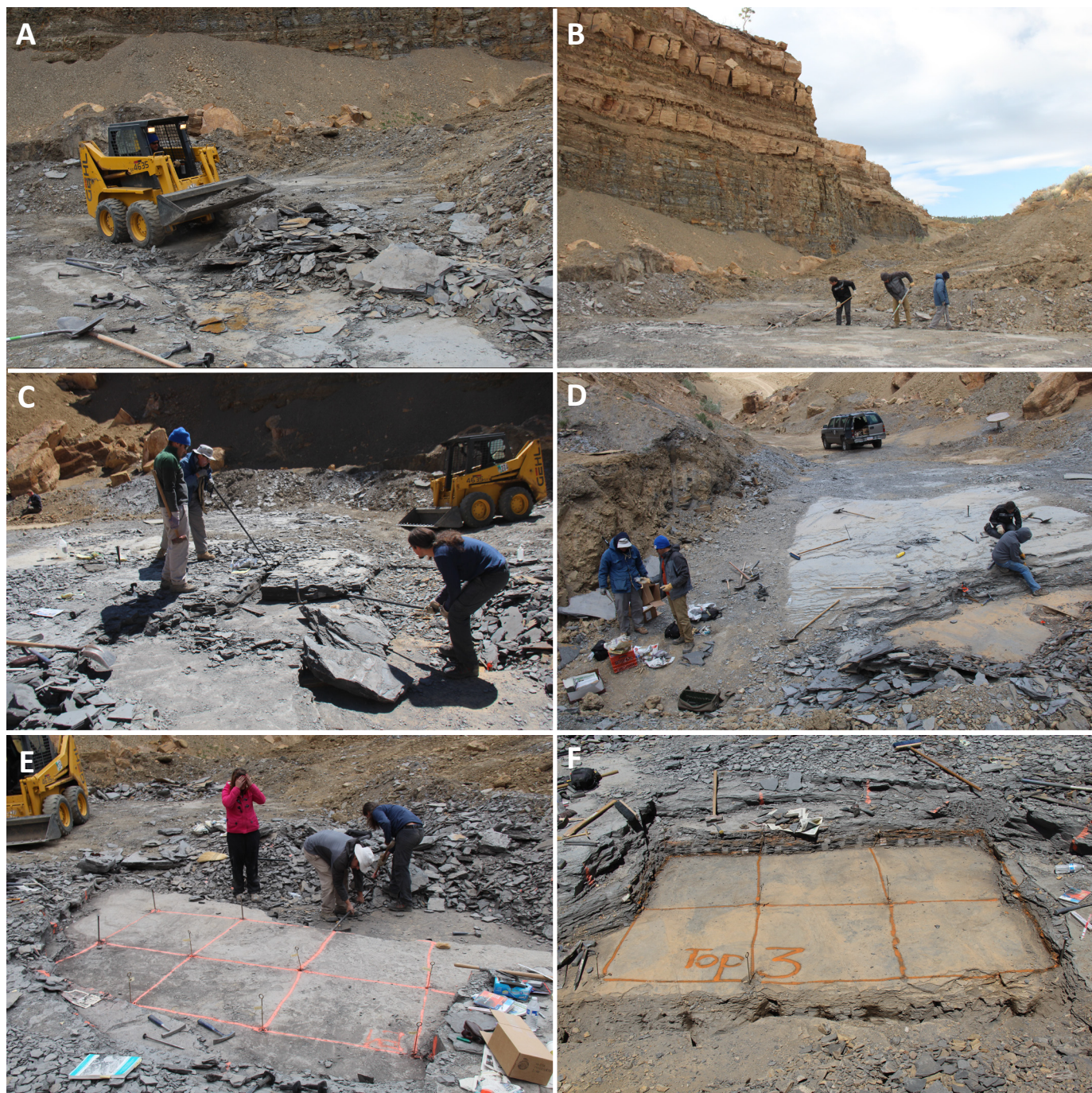


FIGURE 4. Stages of the Kinney Quarry controlled excavation, May, 2014. A. Exposure of the excavation site. B. Clearing of the excavation surface. C. Removing upper layers. D. Quarry view. E. Excavation in progress. Setting up the grid on top of Bed 4. F. Excavation in progress. Grid on top of Bed 3.

and Lucas, 2013). Plant remains are rare, and preservation varies from scraps to relatively large specimens. In most instances, plant remains are isolated and only on one surface of any given hand sample.

Bed 4 of the Kinney excavation (Fig. 1, Bed 4; Fig. 3) is a c. 24 cm-thick, laminated olive gray calcareous siltstone that in places is dark yellowish brown. The bed was subdivided during the excavation into successive layers, but in the present study all were treated as coming from a common source. At the transition from Bed 3 to Bed 4 the rock remains buff in color but lacks Liesegang iron banding. Fossil plant remains are mostly isolated on hand-sample surfaces and generally occur on one side only

of each hand sample. *Dunbarella* is initially rare and consists mostly of small specimens that become more common and larger upward in the bed. The upper part of Bed 4 is of a finely laminated character, splitting to expose large surfaces. Fossil plant remains continue to be confined mainly to one surface of any hand sample and generally occur singly. The remains vary from fragmentary to larger, partially intact specimens.

The collections of the NMNH and those made by Philip Huber, housed at the NMMNHS, contain an additional facies with the plant-fossil compositional characteristics of Bed 4 from the excavation and with a similar *Dunbarella* composition to that bed. They, too, are laminated. However, they are more buff in

color, and the hand specimens differ lithologically from most of those extracted directly from the excavation. The host rock from which these specimens derive splits much more irregularly than Bed 4 specimens from the excavation, so that large, continuous surfaces are rarely exposed. Rather, most specimens are blockier, heavier, and expose a variety of smaller surfaces. We conclude that the coherence of the layers is greater than in Bed 3, perhaps because they are more calcareous or due to a slightly higher clay content. However, given that they are otherwise similar to Bed 4 in biological aspects, we have combined them with the fossil specimens from the excavation of Bed 4.

The c. 1 m thick Bed 5 is similar to excavation Bed 4 (Fig. 1, Bed 5; Fig. 3) in its gray color and lamination. The laminae are somewhat thicker than those of Bed 4, and the shale tends to split into large sheets, thus exposing large, continuous surfaces. Bed 5 contains a much more dense assemblage of *Dunbarella* shells than the other beds of the excavation, and many of these shells are substantially larger than those in the stratigraphically lower beds; some *Dunbarella* are attached to plant fossils, indicating a planktotrophic mode of life for the bivalves (Clark, 1978; Kues, 1992b). The bed will split when weathered into ≤ 1 cm-thick, large plates; plant remains are mainly isolated and confined to a single side of any individual sample. Some of the plant remains are very large and represent everything from intact, large leaves of taxa such as *Dicranophyllum* and *Neuropteris*, to entire small plants such as *Sphenopteris germanica*/*Sphenopteridium manzanitanum*. The single largest plant fossil collected from this bed is a branch of a walchian conifer that is 80 cm long (Looy et al., 2021, this volume). A specimen nearly as large, a partial *Sphenopteris germanica* (*Sphenopteridium manzanitanum*) leaf 73 cm long, was excavated in the quarry floor from Bed 5 but not collected (see Donovan et al., 2021, this volume).

Bed 6 (Fig. 1, Bed 6) is an 80 cm-thick siltstone, olive-gray, indistinctly laminated, and intercalated with claystone layers. On the outcrop it appears as a dense, massive, gray siltstone with irregular, rounded fracture, the splitting planes dictated, in large part, by the presence of plant remains. Invertebrates are sparse. Plant remains are fragmentary and generally sparse and concentrated in the claystone layers.

NMMNHS Collections

Collections from the controlled excavation are housed at the New Mexico Museum of Natural History and Science, Albuquerque, NM. They are kept as separate collections alongside previously collected material from the Kinney Quarry under NMMNHS locality number 345. Plant and animal fossils are housed separately; in this study we focused on the plant fossils, although animal fossils were examined in the event there were plant remains preserved with them, which was occasionally the case.

Additional plant fossils in the NMMNHS collections, collected earlier from the Kinney Quarry by several different individuals but principally Philip Huber, also were examined and counted if their bed-level identity could be established. Because the fossiliferous beds have been recognized as distinct for many years, a substantial number of specimens in the NMMNHS plant-fossil collections are tied to specific beds.

NMNH Collections

The NMNH Kinney Quarry collections were made under the auspices of U.S. Geological Survey geologists Charles B. Read, who made the initial collections, and Sergius Mamay. The collections made by Mamay account for nearly all of those held by the NMNH. They bear USGS Locality Number 10087 and generally were collected without reference to a particular bed. Mamay was assisted by Arthur D. Watt during two visits to the quarry, from May 10 to 16, 1967, and May 10 to 27, 1969.

Over the intervening years, the NMNH collections had

become randomized with respect to bed and collection location within the quarry. Previous curations of the Kinney Quarry collection had segregated some of the better specimens according to their taxonomic affinity, for example, thus mixing specimens from different beds. The NMNH collections were sorted and each specimen was assigned to a bed based on the characteristics as revealed by the excavation. This was possible because of the distinct lithological character and fossiliferous content of the various beds, particularly invertebrate and vertebrate, as clearly revealed by the 2014 controlled excavation. Bed-level differentiation was difficult for certain specimens, particularly separation of Bed 3 and Bed 4, resulting in a group of specimens assigned to a “Bed 3–4 Transition” category. Upon further analysis, however, these specimens proved to be most similar to Bed 4 in plant-taxonomic composition, and in some analyses are combined with that bed.

ANALYSIS OF THE FLORA: METHODS

Fragment Size Analysis

All plant fossils in the Kinney Quarry are allochthonous (transported). Visual inspection of the Kinney Quarry plant remains suggested that the size of the plant-fossil fragments increased systematically from the lower siltstone bed (Bed 2) to the uppermost bed (Bed 5). In order to assess this quantitatively, the size of each plant specimen was measured, and the longest dimension recorded. Comminuted plant debris was excluded. Measurements do not indicate the true maximum size of many of the plant fragments because of limitations imposed by hand-sample dimensions. Nonetheless, the size of the hand samples did not vary substantially from one to the next of the four beds so analyzed. The largest single slabs collected, often in multiple fragments, are from Bed 5, however, reflecting the recognition by collectors of the large size of some specimens in that bed.

Changes in the distribution of fragment size among Beds 2 through 5 of the NMNH collection were analyzed with a one-sided non-parametric implementation of the Kolmogorov–Smirnov test. This test compares cumulative distribution functions and returns a p-value reflecting the probability that both samples (in this case, beds) come from the same underlying distribution. The Kolmogorov–Smirnov test was used instead of a more straightforward comparison of means and standard deviations or a t-test because the constraints on maximum and minimum fragment size are fundamentally different, and maximum fragment size can increase or decrease without any corresponding change in minimum fragment size (see discussion in Schachat et al., 2018). This test was implemented with the `ks.boot` function in the Matching package for R (Sekhon, 2020).

Quantitative Analysis of the Flora

The collections of the NMMNHS and the NMNH were quantified separately (Tables 1–4). Each hand specimen examined was assigned to one of the pre-determined stratigraphic sampling intervals, Beds 1 to 6, with the bulk of the plant remains belonging to Beds 3 to 5. Following the method of Pfefferkorn et al. (1975), as modified and described by Bashforth and Nelson (2015), the top and bottom surfaces of each hand-sample surface were treated as separate sampling quadrats. Plant objects were noted as “present” on that quadrat, regardless of the number of individual plant fragments present. These objects included various taxonomic categories of foliar, axial, and reproductive remains, as well as categories of unidentifiable objects, such as axes, roots and comminuted plant debris. In addition, occurrences of charcoal and various kinds of animal fossils also were recorded. Barren surfaces were recorded. Part and counterpart surfaces were counted as a single quadrat to avoid duplication; thus, a part-counterpart pair accounted for three quadrat surfaces rather than four. The final census, therefore, accounts for all of the surfaces examined.

A quadrat analysis counts the frequency of the occurrence of each plant object among the complete sample of quadrat surfaces. Final percentage occurrences were calculated by using only the informative surfaces; barren surfaces were excluded when considering the total number of quadrats examined. The proportion of barren surfaces in the entire sample does provide, however, an imperfect measure of the density of the plant objects in the original matrix. It is imperfect because when actively excavating, samples barren on both faces are discarded; thus, the proportion of barren surfaces has a limit of 67%, which would be attained if all specimens were part and counterpart (thus 3 surfaces, the part/counterpart not being counted twice), and the opposite sides of both the part and counterpart were barren in all cases. Were there no part-counterpart pairs, the upper limit of barren surfaces would be 50%. Despite this limitation, the percentage of barren surfaces can be used as a metric to compare different paleobotanical collections but not as an absolute measure of the density of plant remains in the host rock. Non-plant categories were not used in the final quantification of occurrence data. Because it was hypothetically possible for each plant-object type to occur on each and every quadrat, the count does not have closure—that is, it does not sum to 100%.

Two matrices were produced for each of the two sample suites. The “basic” matrices (Tables 1 and 2) show all plant objects, counts of their occurrences, and their percent frequency of occurrence. Two additional “reduced” matrices (Tables 3 and 4) were created by eliminating all the non-plant object categories, the unidentifiable plant-object categories such as axes and roots, and plant-objects deemed not to be taxonomically useful for diversity calculations such as “seeds,” “megaspores” or calamitalean stems, the latter because they are non-specific and more taxonomically definitive foliage could be referred to. In compiling the reduced matrices, no adjustments were made to the relative abundances of the plant-object categories; this would not be possible without a quadrat-by-quadrat analysis of category overlaps, and the original data were not recorded at this level of detail.

Diversity (Taxonomic Richness) Analysis

The diversity (by which we mean “richness” in ecological terms) of the identifiably distinct plant-object categories, by sampling level (bed), was first calculated based on the basic matrices without accounting for differences in sample size. The results of that examination indicated a need for rarefaction analysis to account for sample-size differences in order to evaluate more objectively the diversity differences among the bed-level samples. Rarefaction is a statistical method that accounts for differences in original sample size when comparing species richness. It is necessary due to the known relationship between sample size and richness—the more one samples, the more species one finds, up to a point. In rarefaction, a curve is constructed by a process of randomly drawing species from the known, original sample population, creating a species accumulation curve. This is done multiple times to achieve an average richness at any given sample size. When done across original samples, it permits larger original samples to be compared to smaller original samples, at the smaller sample sizes.

Rarefaction analyses were carried out with R software (R Core Team, 2013) and the “rarefy” function of the “vegan” package (Oksanen et al., 2018) using the reduced data matrices. These matrices were selected because they more accurately approximate the biological diversity of the samples. Rarefaction analyses first were run and plotted separately for the NMMNHS and NMNH collections. These were then run and graphed together. Finally, the collections from the NMMNHS and NMNH, attributed to the same sampling beds, were combined

and plotted on a single graph.

Dominance-Diversity Analysis

Dominance-diversity histograms were plotted for Beds 2 to 5, separately for the NMMNHS collections and the NMNH collections. These plots are based on the basic matrices, but eliminating all animal categories and all plant-object categories not identifiable to a taxonomic level of interest (axes, roots, comminuted plant debris; however, seeds, as a single category, were kept as part of the analysis). Histograms are scaled by the percentage of floral elements in each bed that belong to each taxon. Confidence intervals were generated by bootstrapping the data from each bed, with 10,000 replicates. 84% confidence intervals are illustrated because pairwise comparisons of confidence intervals of this size yield a Type I error rate below 0.05 (Gotelli and Colwell, 2011). The bars of the histograms were color-coded by taxon using a colorblind-friendly color palette (Tol, 2019). For ease of comprehension, only the 20 most abundant taxa in each bed are presented. Each dominance-diversity curve was compared to prevailing species abundance models with the “radfit” function of the “vegan” package.

Quantitative Compositional Similarity, Exploratory Analyses

Exploratory statistical analyses to assess bed-level plant assemblage quantitative similarity were carried out using R software (R Core Team, 2013; see McCune and Grace, 2002, for a discussion of these techniques) and the “vegan” package (Oksanen et al., 2018). Two kinds of analyses were carried out, using the reduced matrices. The reduced matrices were chosen, as above, because they more closely approximate actual biodiversity without being inflated by taxonomically non-specific categories. The NMMNHS and NMNH bed-level samples were included separately in these analyses, using a combined reduced input matrix.

The first analysis of the bed-level similarity was computed using Unweighted Pair Group Cluster Analysis (UPGMA; method = “average” in function “hclust,” “vegan” package). UPGMA is a method of hierarchical clustering that generates a non-reticulate dendrogram, which displays the relationships among the samples. Data were standardized by dividing the abundance of each taxon by row totals in the data matrix. Bray-Curtis dissimilarity was used for the distance matrix.

The second type of analysis was an ordination, using Non-metric Multidimensional Scaling (NMDS) set to two dimensions (“metaMDS” function, “vegan” package). 84% confidence ellipses were generated in the NMDS plot, again following the logic of Gotelli and Colwell (2011), to quantify the uncertainty surrounding the relative positions of each bed in the plot. The per-quadrat occurrence data from the informative quadrats in each bed were resampled 500 times following the procedure outlined by Schachat et al. (2020). Because occurrence data were collected as per-taxon lists without noting the exact quadrats in which each taxon occurred, each occurrence had to be randomly assigned to a quadrat before the quadrats could be resampled. The data first were standardized by dividing the abundance of each taxon by the row totals in the data matrix.

A Bray-Curtis dissimilarity matrix then was calculated as the distance metric. The coordinates of the resampled data in the NMDS plot were used to generate the confidence ellipses for each bed. NMMNHS Bed 1 was excluded from NMDS because it only contains nine informative quadrats. Because this procedure includes two sources of randomness, the random assignment of occurrences to quadrats and the random initial configuration of the NMDS, the procedure was repeated six times to permit examination of the role of this randomness in determining the relationships between the beds.

ANALYSIS OF THE FLORA: RESULTS

Fragment Size Analysis

Among Beds 2 through 5 of the NMNH collection, minimum fragment size changes negligibly, whereas maximum fragment size changes noticeably, driving an increase in mean fragment size from the bottom to the top of the section (Fig. 5). The Kolmogorov–Smirnov test confirms that the observed changes in fragment size are significant. P-values for differences in fragment size between adjacent beds range from 0.017* to <0.001***. P-values for differences in fragment size between non-adjacent beds are even more highly significant, all below 0.00001***. As shown in Table 5, the standard deviation in fragment size also shows a systematic pattern of change, with increasing variability toward the top of the siltstone bed sequence, consistent with a changing range of fragment size from the lower to the upper plant-fossil-bearing beds.

Quantitative Analysis Of The Flora

For both the basic and reduced matrices, the actual occurrence counts for each plant-object category are presented, as are its frequency as a percentage of the entire suite of informative quadrats. In the NMMNHS analysis (Tables 1 and 3), samples from different excavation grids have been organized by bed number, from Bed 1 to Bed 6, representing the sequence from the bottom to the top of the plant-bearing siltstone. The actual counts of abundance for each plant-object category are presented, as is its frequency, as a percentage of the entire suite of informative quadrats. The NMMNHS collections include samples from each of the 6 identified fossiliferous beds; those from the NMNH (Tables 2 and 4) include samples only from Beds 2 to 5. However, because the NMNH collections were made more than 45 years earlier than those from the NMMNHS controlled excavation, in a different area of the quarry, they possibly reflect slightly different original environmental and depositional (facies) conditions.

The NMNH collections are larger than those held by NMMNHS. In addition, sample sizes by bed vary between and within the two collections, although the bulk of the collections in each museum comes from Beds 3 to 5. The number of informative quadrats (Total Quadrats minus Barren Quadrats) in the NMMNHS collections are the following: Bed 1: 9, Bed 2: 30, Bed 3: 306, Bed 4: 115, Bed 5: 199, Bed 6: 53. In the NMNH collections, the following informative quadrats were counted: Bed 2: 51, Bed 3: 503, Bed 3/4 (= Bed 4): 116, Bed 4: 858, Bed 5: 308. A chi-squared test was performed as a test

of homogeneity to evaluate differences in sample sizes by bed between the two collections. This test was performed with the base-R function `chisq.test()`. The results of this analysis indicate that sample sizes by bed do not vary significantly between the two collections ($p = 0.22$).

The proportion of barren quadrats provides an imperfect measure of the sparseness of the fossils in the matrix, as noted above. Because part and counterpart faces were counted only once, it is possible (and, for Kinney, in fact likely) that both counter faces were barren. Thus, particularly in large collections where part-counterpart specimens may make up a substantial part of the collection, the percentage of barren surfaces may exceed 50%. This happened in only one instance, Bed 3 of the NMMNHS collections. In all others, the proportion of barren surfaces varied between 41% and 50%, with an average across all collections, excluding NMMNHS Bed 3, of 45%.

The NMMNHS collections contain 62 plant-object categories. The reduced matrix contains 47 plant-object categories, as operational taxonomic units. The larger NMNH collections contain 85 plant-object categories, ranging from identified taxa or morphotypes, to roots, comminuted plant debris, and axes. When reduced to operational taxonomic units, in the reduced matrix, this accounts for 74 plant-object categories.

No charcoal was identified in the NMMNHS collections, and only one occurrence was noted in the NMNH collections. Comminuted plant debris also was rare, occurring at a frequency of 0–1.7% in all but one of the bed-level samples, where it reached 4.2%. Fish remains were most abundant in the lowermost units, Beds 1 and 2. The remains of shelly invertebrates were common, but particularly noteworthy is that of *Dunbarella*, an indicator of fresh-to-brackish conditions, which appears in abundance in Beds 4 and 5. In fact, in Bed 5, it is the single most common type of fossil in the plant-fossil collections. *Dunbarella* is present but rare in Bed 3, and absent from the plant-fossil samples collected from Beds 1 and 2.

Diversity (Taxonomic Richness) Analysis

A plot of the relationship between plant-object categories and informative-quadrat sample size (Fig. 6; Table 6), computed from the basic matrix, revealed a positive relationship, as expected. An examination of the graph shows a proportional diminishment in the number of objects identified at larger sample sizes. When the squared count, rather than the raw count, of identified plant-objects in each bed is regressed against the number of informative quadrats, R^2 increases from 0.80 to 0.88.

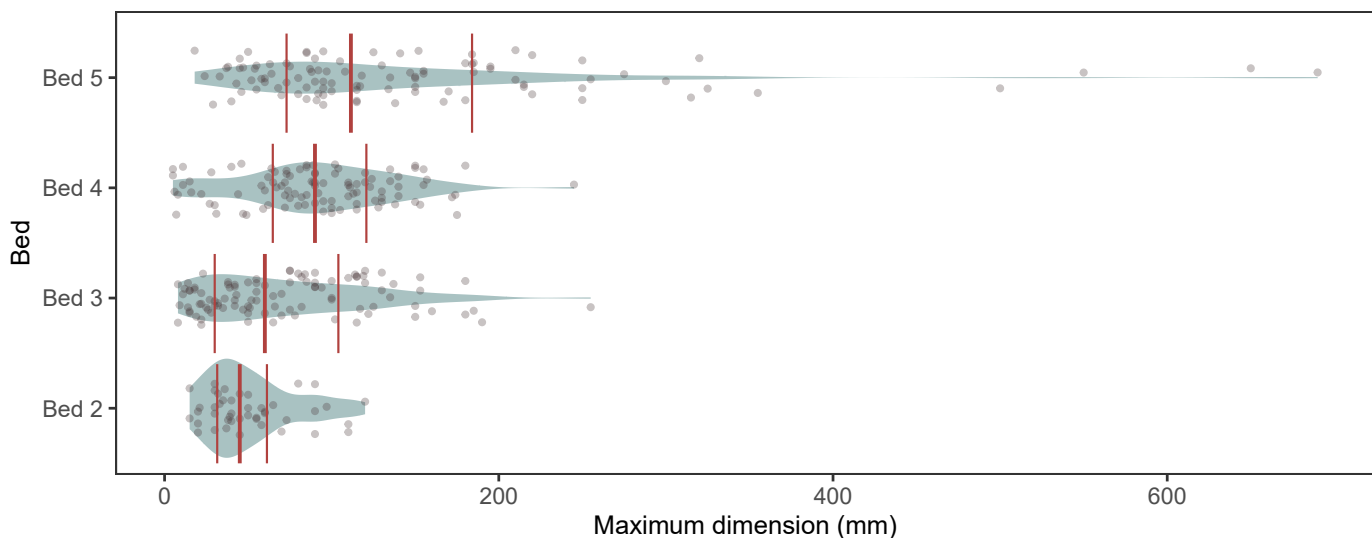


FIGURE 5. Average maximum dimension of specimens on hand samples, by Bed level.

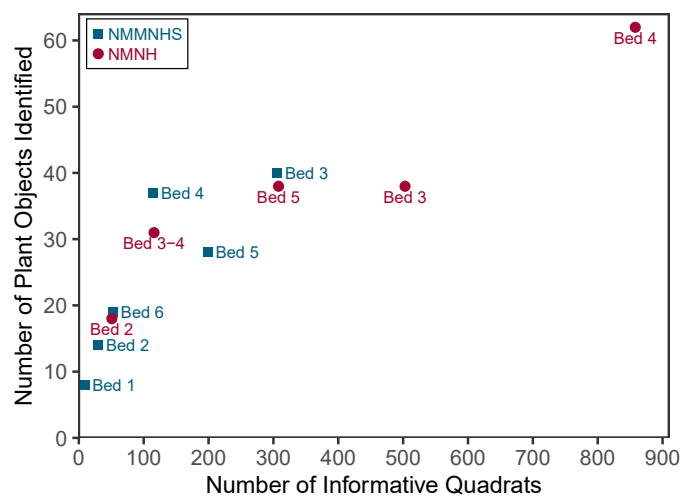


FIGURE 6. Diversity (plant-object richness) as a function of number of informative quadrats (sample size).

TABLE 5. Average fragment size (maximum dimension) by bed, National Museum of Natural History collections.

	Bed 2	Bed 3	Bed 4	Bed 5
Mean	51.3	72.0	91.2	146.0
STD Sample		50.6	46.1	120.0
STD Pop	26.7	50.3	45.8	119.4

TABLE 6. Sample size by bed, National Museum of Natural History collections. Presented graphically in Figure 4.

BED	Informative	# of Objects
NM 6	53	19
NM 5	199	28
US 5	308	38
NM 4	115	37
US 4	858	62
US 3-4	116	31
NM 3	306	40
US 3	503	38

It is clear that diversity comparisons among and between bed-level samples need to be constrained by rarefaction analysis.

Rarefactions were performed for each of the bed-level samples from both museum collections (Fig. 7); those illustrated here are based only on the reduced matrices (Tables 3 and 4). The analyses for the three most abundant collections, from Beds 3, 4, and 5, are of the greatest interest because of their large sample size.

In the large NMNH collections, Bed 4 has much higher taxonomic richness than, sequentially, Bed 5 and Bed 3 (Fig. 7A).

In the NMMNHS samples (Fig. 7B), when compared at the sample size set by the smallest of the collections, which is Bed 4, species richness is greatest in Bed 4, followed sequentially

by Bed 3 and Bed 5. The apparent greater richness of Bed 3 is a consequence of the larger sample collected from that unit. The NMMNHS collections also have the largest of the small samples, which include Bed 6. When compared at Bed 6 sample size, the order of taxonomic richness remains unchanged, with Bed 6 having approximately the same taxonomic richness as Bed 3.

The NMNH and NMMNHS samples are compared directly in Figure 7C. A combined analysis (Fig. 7D), in which counts from the two data sets were added together, reveals that Bed 4 has the highest combined richness, followed sequentially by Bed 3 and Bed 5. However, at smaller, but not insignificant sample sizes of ~250 informative quadrats, Bed 3 and Bed 5 have indistinguishable richness, with Bed 5 appearing to approach an asymptote as sample size increases.

The maximum richness attained in any of the analyses was found for Bed 4 in the combined analysis. In that bed, a taxonomic richness of slightly more than 90 operational taxonomic units was found at a sample size of approximately 950 informative quadrats. Bed 3 has a maximum combined sample richness of approximately 45 taxa at a sample size of about 750 informative quadrats. The maximum combined taxonomic richness of Bed 5, approximately 35, was reached at approximately 500 informative quadrats.

Dominance-Diversity Analysis

Dominance-diversity curves were plotted, as histograms, for Beds 1 to 6 for each of the collections (Fig. 8), based on the reduced matrices (Tables 3 and 4). The most abundant plant-object categories are labelled directly on the graph. In all instances, the typical hollow curve was found. The sequence of taxa varies from one bed and one collection to the next. Only rarely do replicates have the same dominant taxon. However, the first several taxa in the rank order often are the same.

When the dominance-diversity curves were compared to theoretical models, the three curves with fewer than 45 specimens and fewer than 16 taxa (NMMNHS Bed 1, NMMNHS Bed 2, NMNH Bed 2) conformed best to the null, broken-stick model. For all other curves, which contain 47 to 720 specimens and 16 to 54 taxa, the null model was rejected in favor of the Mandelbrot, Zipf, or lognormal models. These model comparisons demonstrate the existence of a long tail of rare taxa in all dominance-diversity curves that contain enough specimens to show one.

Samples from Beds 1 (Fig. 8A), 2 (Fig. 8B), and 6 (Fig. 8A) are the least diverse, which is an expectation based on their small sample sizes. The number of informative quadrats was 9 (Bed 1-NMMNHS), 30 (Bed 2-NMMNHS), 51 (Bed 2-NMNH), and 53 (Bed 6-NMMNHS), respectively. For Bed 2 (Fig. 8B) the order of importance differs between the NMMNHS and NMNH collections. Four of the five most important taxa are shared: the sphenopsid foliage *Phyllothea* sp. (3rd vs. 1st), the conifer *Walchia piniformis* (3rd vs. 2nd), calamitalean stem remains (3rd vs. 3rd), and the pteridosperm *Neuropteris ovata* (1st vs. 4th). The second most frequently occurring taxon in the NMMNHS collection, *Dicranophyllum* sp., is the fifth most important taxon in the NMNH collection (tied with four other taxa). Overall, the flora of Bed 2 appears to be reasonably similar in composition and dominance between the two samples, given the small sample size. It can be characterized as a strongly mixed assemblage of xeromorphic drought-tolerant plants and taxa characteristic of soils with persistently high water tables.

Bed 3 (Fig. 8C), one of the three largest samples, has a combined sample size of 809 informative quadrats. The richness of taxa is comparable in the NMMNHS and NMNH samples, 38 and 37, each sample having a long tail of rarely occurring taxa, found in all the samples of sufficient size. Both collections are dominated by *Neuropteris ovata*, with calamitalean stems,

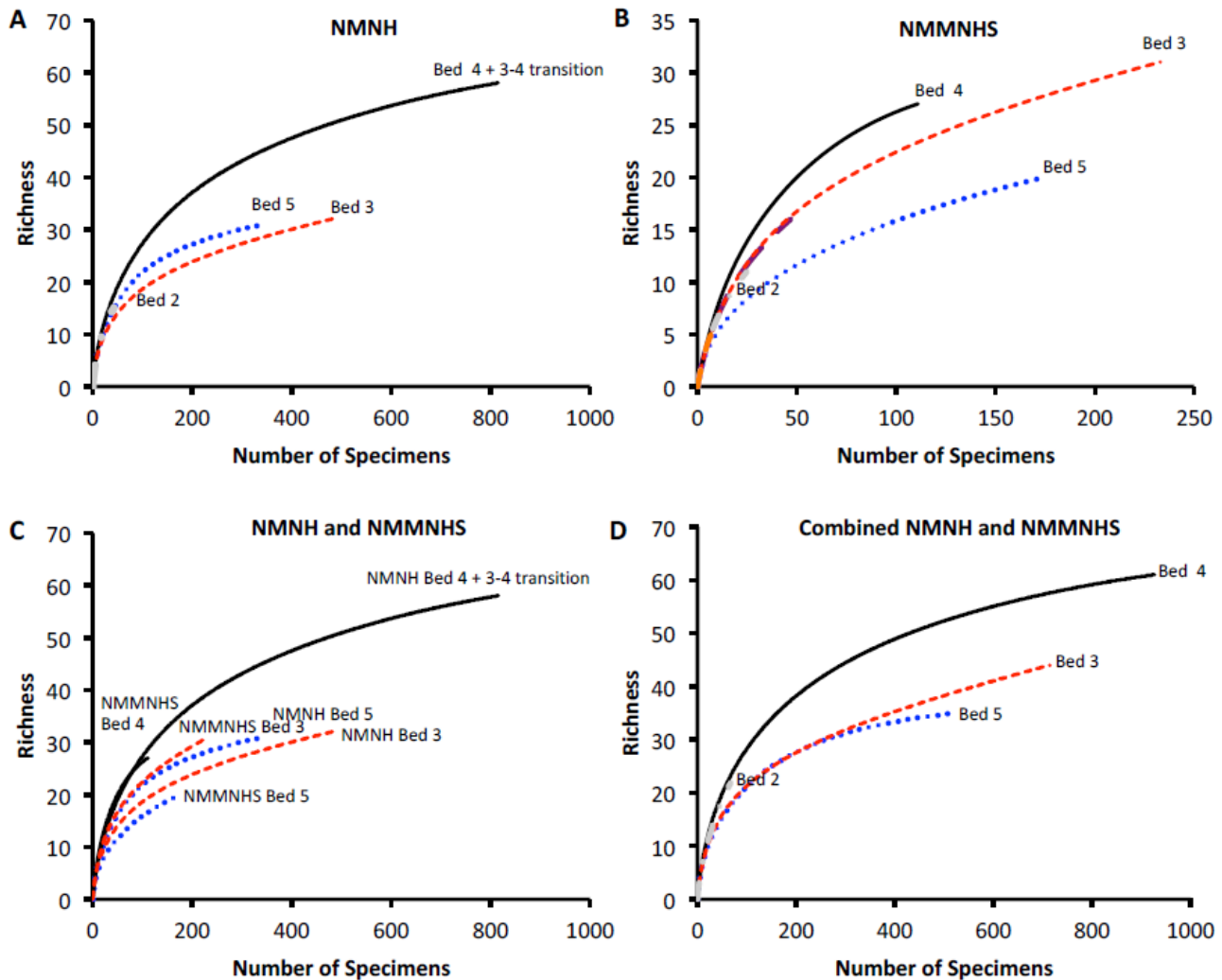


FIGURE 7. Rarefactions of Kinney floristic, plant-object richness based on reduced data sets. A. NMNH (USNM) Collection. B. NMMNHS Collections. C. NMNH and NMMNHS Collections in joint plot. D. NMNH and NMMNHS Collections combined by Bed.

Phyllothea sp., marattialean fern foliage, cordaitalean foliage, and seeds among the 10 most common elements in each collection. The noeggerathialean *Charliea manzanitana* is the second most common element in the NMNH collection, and ranks 11th in that of the NMMNHS. These taxa, therefore, account for most of the assemblage in each collection. Walchian conifers are uncommon, occurring at frequencies of about 4.5% in the NMMNHS collection, and 2% in that of the NMNH. This sample is dominated quantitatively, in both collections, by taxa that require high soil moisture. There is, however, a significant component of more meso- to xeromorphic elements, considered to be drought-tolerant (see comments in accompanying atlas of common fossil plant taxa in each bed, Donovan et al., 2021, this volume). This is demonstrated most clearly by the frequency of *Charliea manzanitana* in the NMNH collection, which may reflect collection bias by the USGS collectors, who were focused on the discovery of new species (revealed clearly by comments in Sergius Mamay's 1960s field notes: *Charliea* was first described from the Kinney Quarry). The considerable spatial distance between the location in the quarry of the NMNH and NMMNHS collections (Fig. 2) also may underlie this difference and reflect microhabitat heterogeneity on the original landscape. The character of the enclosing rock matrix is both distinctive

and essentially identical between these two collections, lending confidence to the bed identity.

The NMMNHS and NMNH collections from Bed 4 (Fig. 8D) differ in important ways but also share important similarities. The most conspicuous difference is in the sizes and diversities of the two collection suites. The NMMNHS collection consists of 115 quadrats, and 35 taxa. In contrast, the NMNH collection consists of 858 quadrats and 62 taxa, resulting in a longer tail of rare taxa. There is a difference in dominance, with *Neuropteris ovata* being the most frequently occurring taxon in the NMMNHS collections; this is a typical wetland species, and similar to the relative importance of taxa in the Bed 3 collections from the same location in the quarry. Of the remaining 10 most frequently occurring taxa, however, there is considerable overlap between the two collections, including a roughly similar order of importance among the suspected lyginopterid pteridosperm *Sphenopteris germanica* (= *Sphenopteridium manzanitanum*), walchian conifers, the coniferophyte *Dicranophyllum readii*, and seeds. The only conspicuous wetland elements, other than *N. ovata*, are marattialean fern remains (including *Danaeites* sp.). Top 10 elements not shared among the NMMNHS and NMNH collections are almost all either mesomorphic or xeromorphic taxa such as *Charliea manzanitana*, cordaitalean foliage, the

pteridosperm *Mixoneura subcrenulata*, and the peltasperm *Peltaspernum*. Small filiclean ferns and the calamitalean foliage *Annularia carinata* occur in the lower ranks of the top 10 in the NMNH collection. Thus, the Bed 4 flora has a conspicuous component of drought-tolerant taxa and marks the first abundant appearance of *S. germanica*.

The Bed 5 (Fig. 8E) samples represent the topmost collections from the laminated siltstone units. The NMNH collection is approximately 1/3 larger than that of the NMMNHS and has 25% more identified plant-object categories. The object-class/taxonomic composition of the most abundant taxa is similar for the two collections. The NMMNHS collections are dominated by *Sphenopteris germanica*, whereas those of the NMNH are dominated by *Dicranophyllum* cf. *readii*, followed by *Sphenopteris germanica*. The sequence of taxa after that is quite similar for the more abundant forms, including *Neuropteris ovata*, walchian conifers, cordaitalean foliage, seeds, and calamitalean stems. Top 10 elements not shared between the two collections include *Charliea manzanitana*, *Dicranopyllum* sp., the pteridosperm *Neurodopteris auriculata*, and pteridosperms *Mixoneura/Odontopteris* spp. from the NMMNHS collections, and *Mixoneura subcrenulata* from the NMNH collections. The high occurrence frequency of *Dicranophyllum* in the NMNH collections again may be evidence of collection bias. As with *Charliea*, this was a newly identified taxon at the time, and the USGS collectors were focused on finding new types of plant fossils, and thus may have “over collected” that plant; it was not unusual for an entire bed that contained a new type of plant to be heavily collected, especially when the objective of the fieldwork was to find fossil plants of a type not previously known to science. Taking that into consideration, the sequence of taxon dominance between the two collections is remarkably similar. The flora, in either case, is composed dominantly of mesomorphic to xeromorphic, presumably drought-tolerant plants, with a moderate admixture of less tolerant, more hygromorphic taxa, such as *N. ovata* and calamitaleans. Even the rare elements of the assemblages are mainly drought-tolerant forms.

Quantitative Compositional Similarity, Exploratory Analyses

Examples of many of the plant-fossil taxa mentioned below are illustrated in the companion paper to this by Donovan et al. (2021, this volume). The drought-tolerances of these taxa, based on many lines of evidence from the paleobotanical literature, are summarized there as well. These sources of evidence include the gross morphology of the plants, their physiological properties as inferred from anatomical and modeling studies, taxonomic co-occurrence patterns, and co-occurrences between specific taxa and specific kinds of sedimentological conditions.

Exploratory analyses of the Kinney matrices were carried out by two standard means, cluster (UPGMA), and ordination (NMDS, stress value = 0.15) analyses. The results of these analyses are similar. There were no samples in the NMNH collection that could be assigned unambiguously to Bed 6, so there is no representation of that in the analyses. In the UPGMA (Fig. 9A), one principal cluster consists of Beds 1, 2 and 3, and the other of Beds 4 and 5. The NMDS (Fig. 10) differs from the UPGMA in that the Bed 2 samples from NMNH and NMMNHS cluster adjacent to one another, rather than being in separate clusters, as in the UPGMA.

The most notable anomaly in the analyses is the relationship of NMNH Bed 2 and NMMNHS Bed 2, which are close together in the NMDS but do not cluster together in the UPGMA. NMMNHS Bed 2 is part of the Bed 1–2–3 UPGMA cluster, whereas NMNH Bed 2 weakly clusters with NMMNHS Bed 6, and these two assemblages (USNM Bed 6 and NMMNHS Bed 6) together are closest in quantitative affinity with the Bed

4–5 group—but again at a low level of similarity. Examination of the dominance-diversity curves (Fig. 8) suggests that the distinctiveness of NMNH Bed 2 (Fig. 8B) and NMMNHS Bed 6 (Fig. 8A) resides in quantitative composition, rather than in presence-absence composition. There are substantial similarities between USNM Bed 2 and the assemblages in the Bed 1–2–3 group. To investigate this further, the UPGMA analyses were rerun without NMMNHS Bed 6, and with the various NMNH Bed 4 categories (Bed 4, Bed 3–4 transition, Bed 4 + Bed 3–4 transition) combined (Fig. 9B). The results are substantially the same as in the full analysis.

In the NMDS plot (Fig. 10), NMMNHS Beds 6 falls between the Beds 4–5 and Beds 2–3 groups. NMNH Bed 2 falls between NMMNHS Beds 6 and 2, and is part of a Beds 2–3, group. Also of interest in the ordination, when confidence ellipses are calculated (the solid ovals in Fig. 10), there is no overlap among the samples from the NMMNHS and NMNH collections, even if drawn from the same bed. Indeed, despite the superficial lithological similarity between NMMNHS Beds 4 and 5 in the 2014 excavation, the plant assemblages from those beds are not nearest neighbors.

The anomalous relationship of NMNH Bed 2 and NMMNHS Bed 2 in the UPGMA plot can potentially be explained by the structure seen in the NMDS plots, in which the beds form a circular pattern completely lacking in directionality or strongly differentiated multi-bed clusters. The lack of overlap between the confidence ellipses for any beds, recovered in all six iterations of the NMDS procedure, confirms their relative positions and thus supports the pattern that the beds form. The beds that cluster together in the UPGMA dendrogram—such as NMMNHS Bed 3, NMMNHS Bed 2, and NMNH Bed 2; and NMMNHS Bed 5 and NMNH Bed 5—plot closely together in NMDS space.

Dominance by, or sub-dominant abundance of, *Neuropteris ovata* is the most conspicuous shared characteristic of assemblages in the Bed 1–2–3 group. Also important in Beds 1–2–3 are the hygromorphic (drought-intolerant) calamitalean sphenopsids, in particular the foliage-type *Phyllothea* sp., and marattialean fern foliage. Plants thought to be more drought tolerant in Beds 1–2–3 include *Dicranophyllum* sp., cordaitalean foliage, and the noeggerathialean *Charliea manzanitana*. Xeromorphic walchian conifers are a significant part of both Bed 2 collections (Fig. 8B), but are much reduced in abundance in Bed 3 (Fig. 8C).

The 10 most common elements in NMNH Bed 2 (Fig. 7B) are similar to those of the Bed 1–2–3 group, but not dominance by *Neuropteris ovata*, which is the main characteristic uniting the other Bed 1–2–3 assemblages. In NMNH Bed 2 (Fig. 8B), *N. ovata* is common (4th in importance, and > 10% frequency of occurrence) but not the plant-object category of highest occurrence frequency. The assemblage is dominated by *Phyllothea* sp., and also has abundant calamitalean stem remains. *Walchia piniformis* is the second most abundant taxon, and both *Dicranophyllum* and cordaitalean foliage are among the 10 most frequently occurring plant objects.

The Bed 4–5 group of assemblages is characterized by a shift to a greater frequency of xeromorphic taxa, generally considered to be tolerant of seasonal drought. Most conspicuous of these is *Sphenopteris germanica* (= *Sphenopteridium manzanitanum* of Mamay, 1992). This group includes other taxa such as walchian conifers, cordaitalean foliage, and *Charliea manzanitana*. However, the taxa typical of high-moisture substrates continue to be present, particularly marattialean fern foliage and the pteridosperm *Neuropteris ovata*. The latter is the most frequently encountered plant-object in NMMNHS Bed 4 (Fig. 8D), and of third importance in NMNH Bed 5 (Fig. 8E), no doubt contributing to their proximity in both the ordination and cluster analyses.

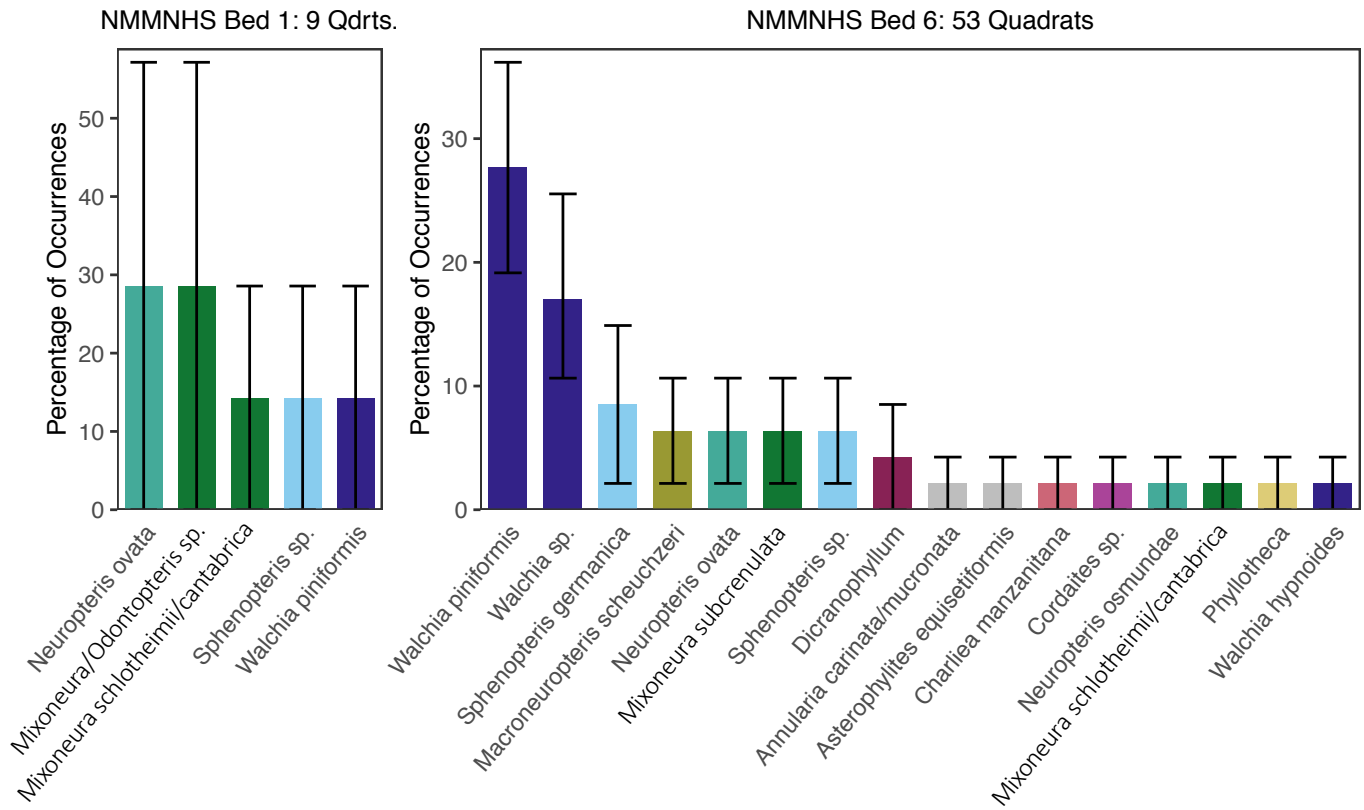
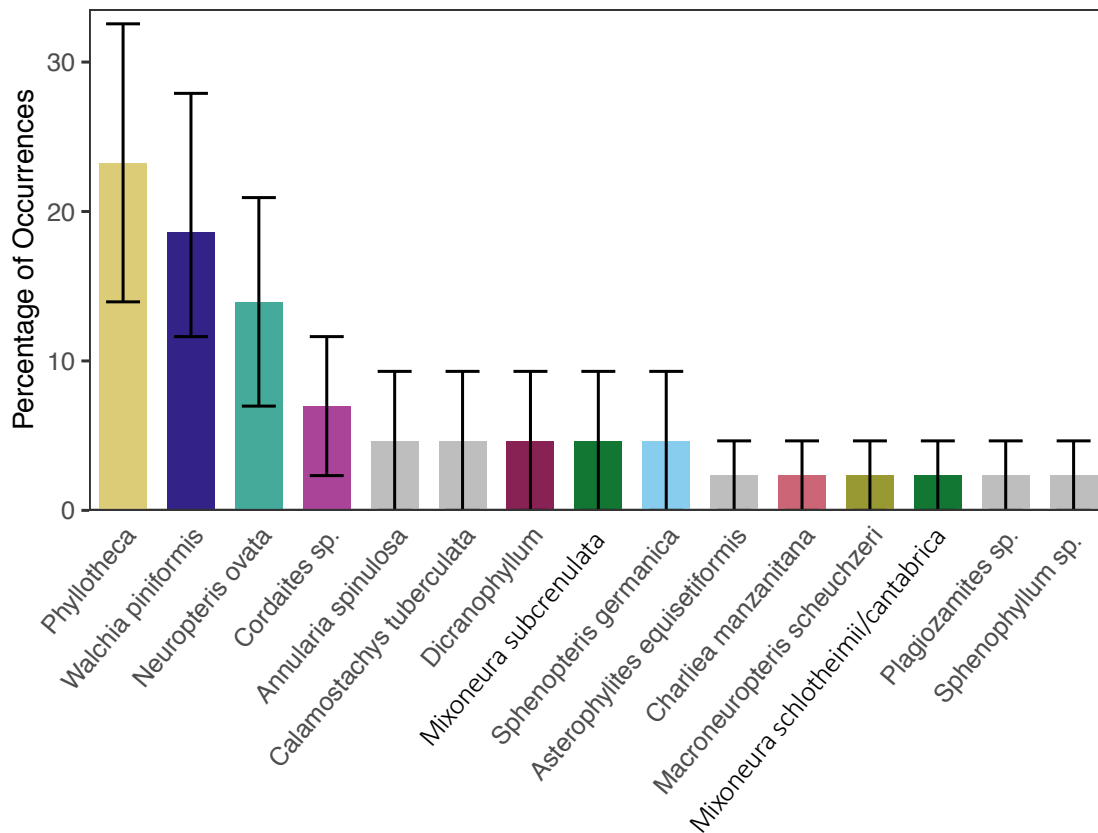


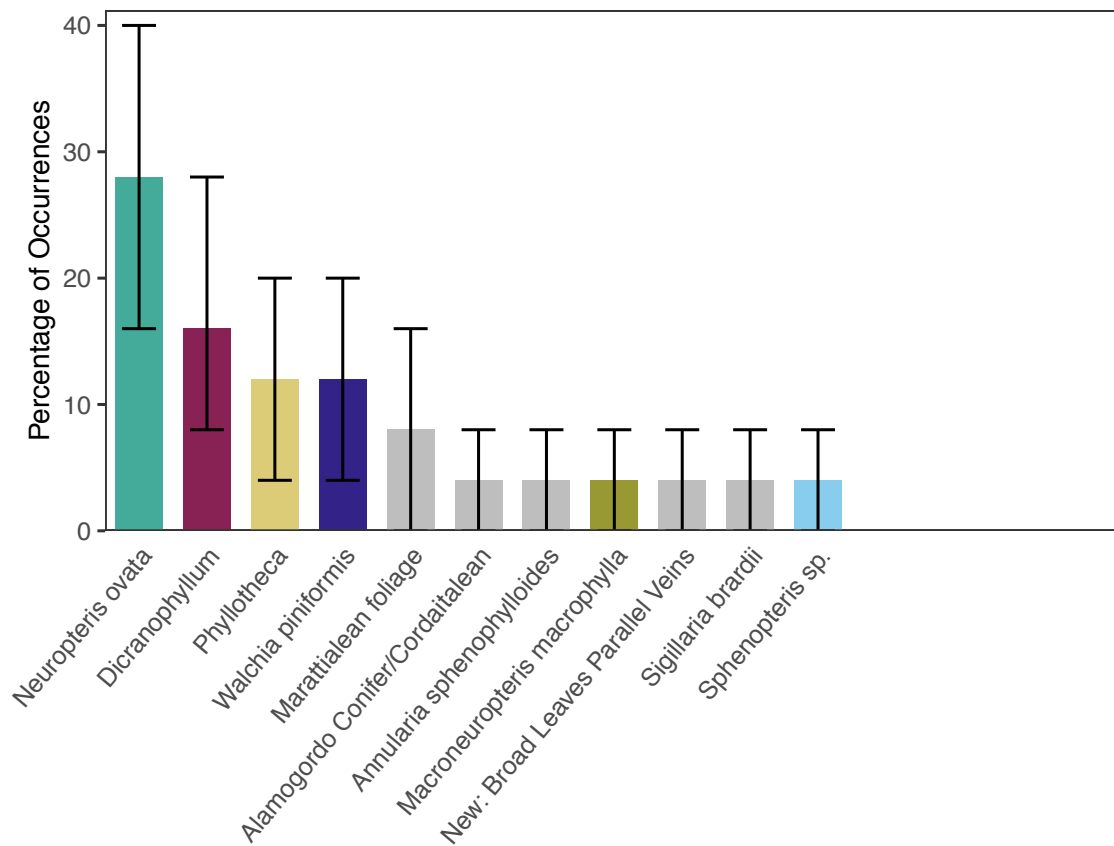
FIGURE 8. Dominance-Diversity curves by Bed by museum collection, in five parts. Confidence intervals shown. Part 1: The lowermost bed, NMMNHS Bed 1 & the uppermost bed, NMMNHS Bed 6.

FIGURE 8. (continued facing page) Dominance-Diversity curves by Bed by museum collection, in five parts. Confidence intervals shown. Part 2: NMNH Bed 2 & NMMNHS Bed 2.

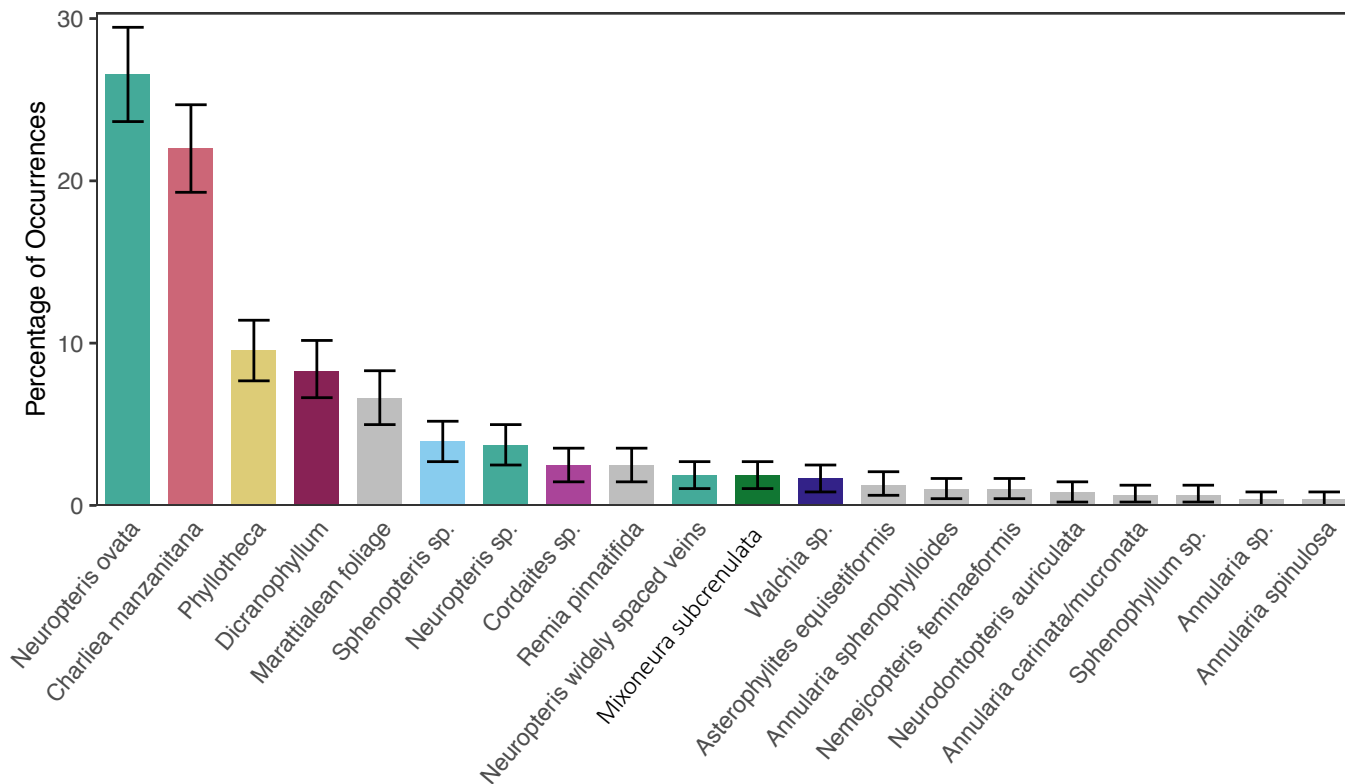
NMNH Bed 2: 51 Quadrats



NMMNHS Bed 2: 30 Quadrats



NMNH Bed 3: 503 Quadrats



NMMNHS Bed 3: 306 Quadrats

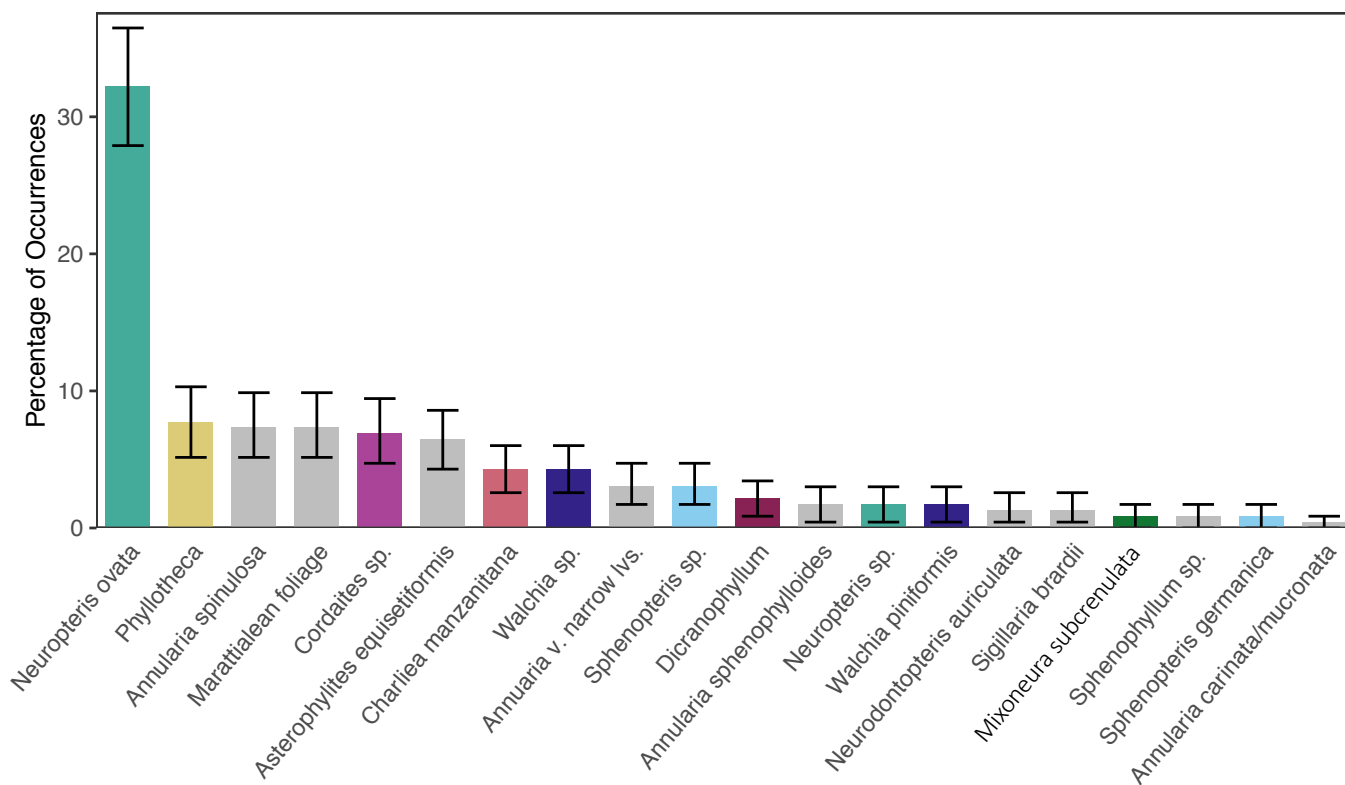
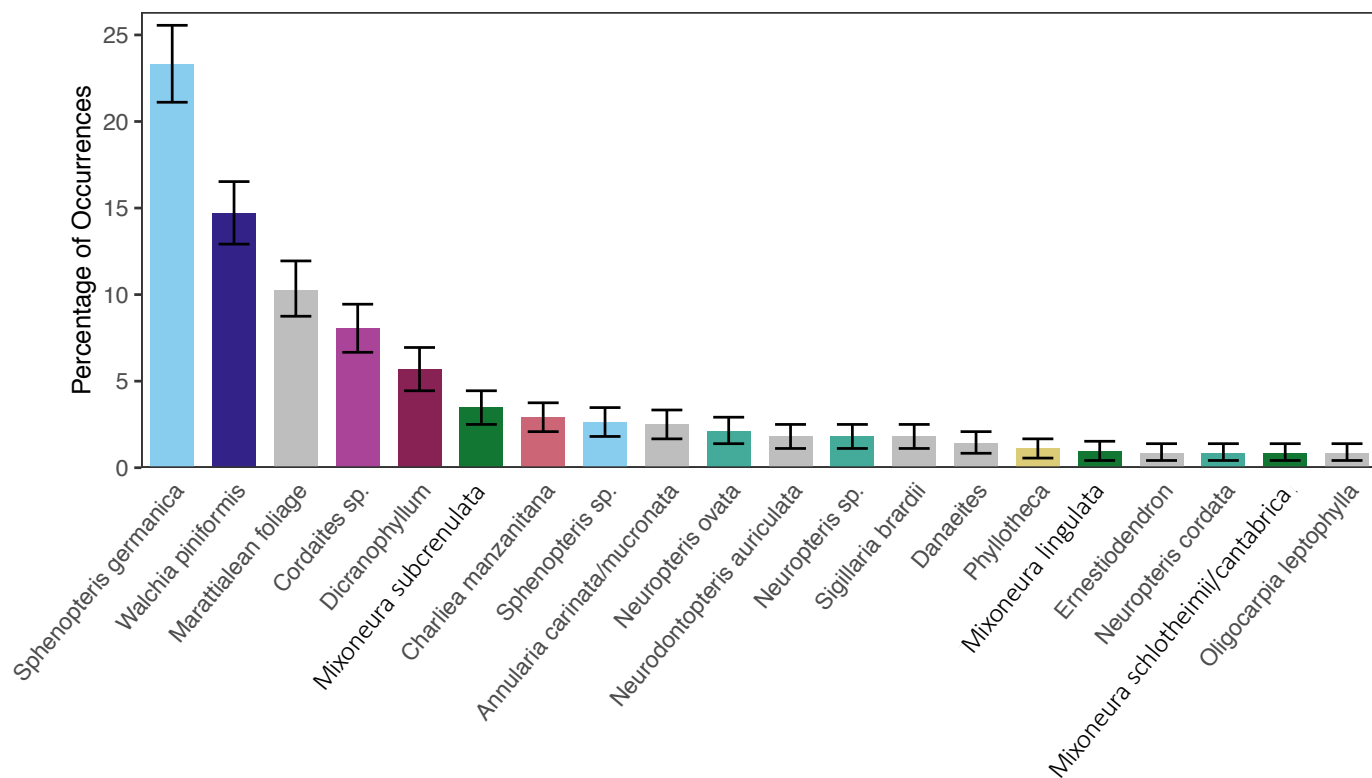


FIGURE 8. (continued) Dominance-Diversity curves by Bed by museum collection, in five parts. Confidence intervals shown. Part 3: NMNH Bed 3. & NMMNHS Bed 3.

NMNH Bed 4: 858 Quadrats



NMMNHS Bed 4: 115 Quadrats

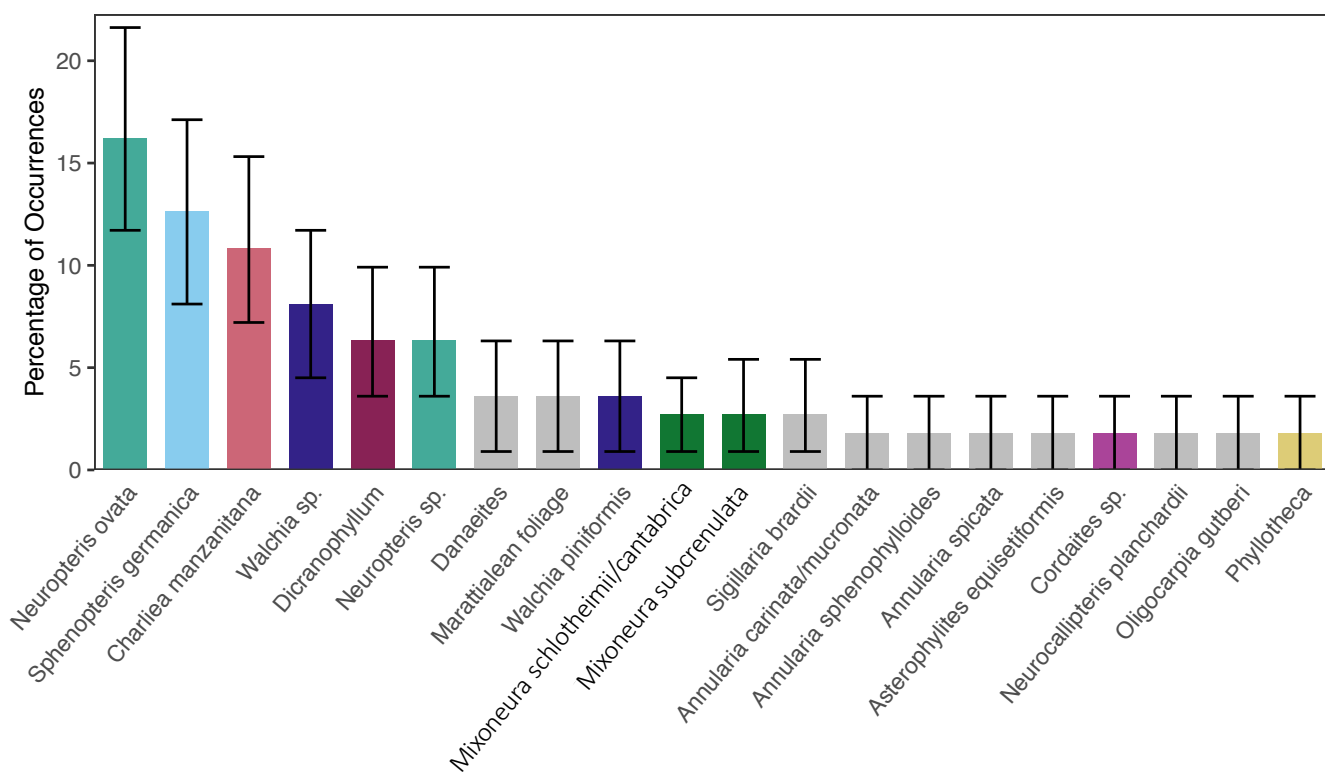
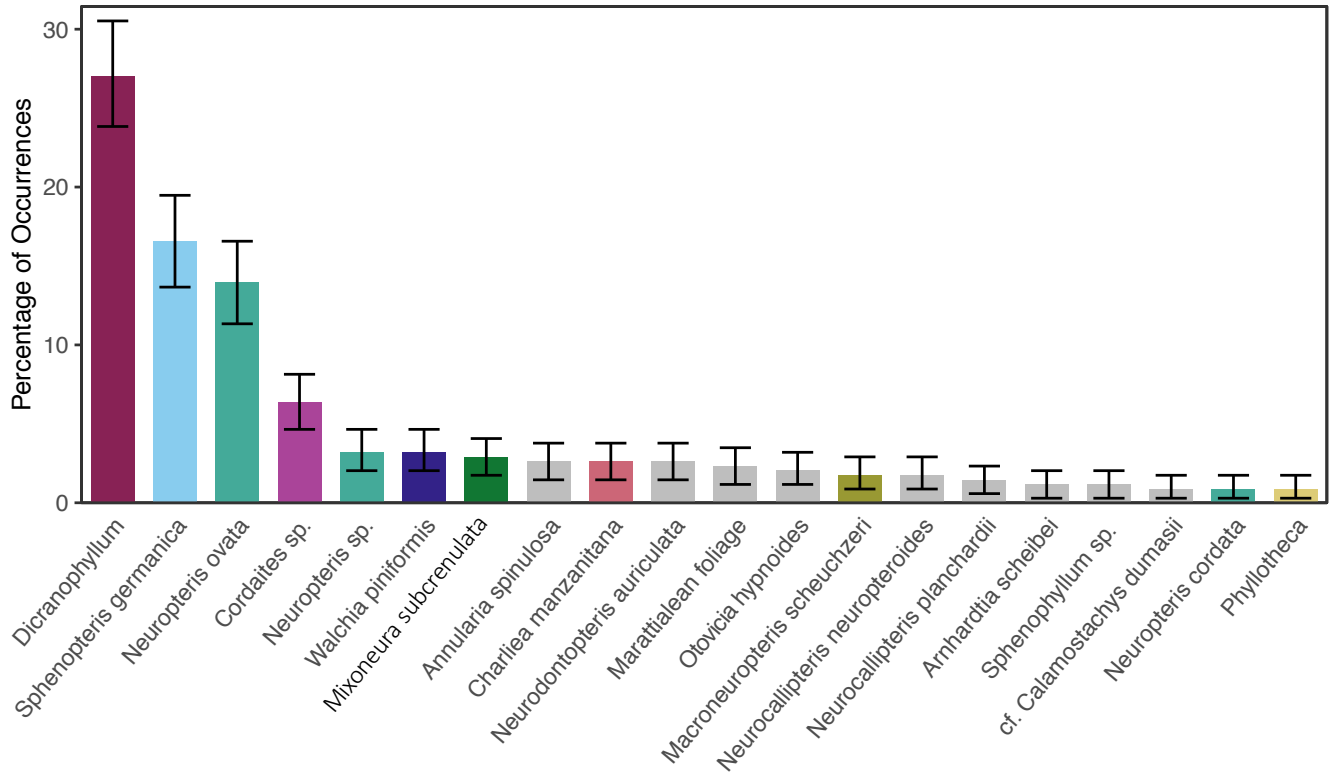


FIGURE 8. (continued) Dominance-Diversity curves by Bed by museum collection, in five parts. Confidence intervals shown. Part 4: NMNH Bed 4 & NMMNHS Bed 4.

NMNH Bed 5: 308 Quadrats



NMMNHS Bed 5: 199 Quadrats

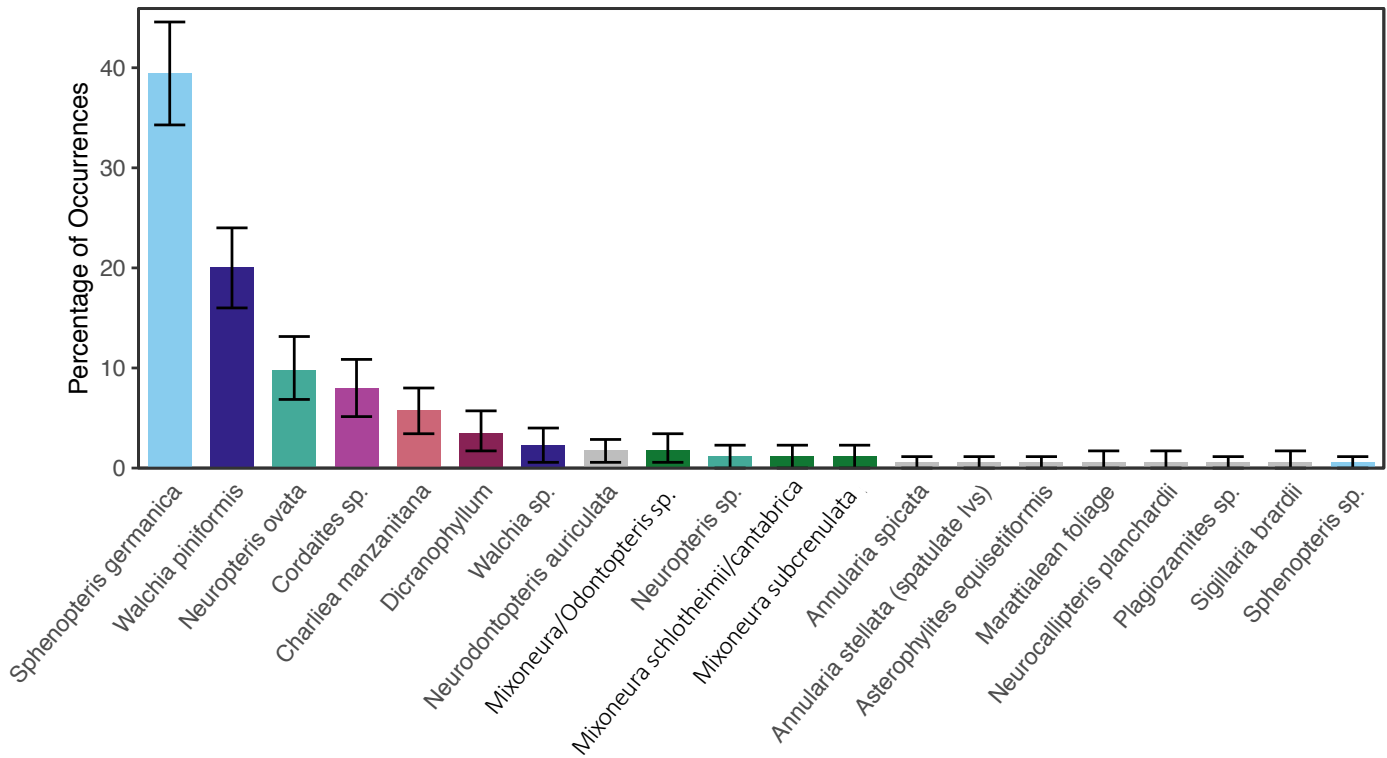


FIGURE 8. (continued) Dominance-Diversity curves by Bed by museum collection, in five parts. Confidence intervals shown. Part 5: NMNH Bed 5 & NMMNHS Bed 5.

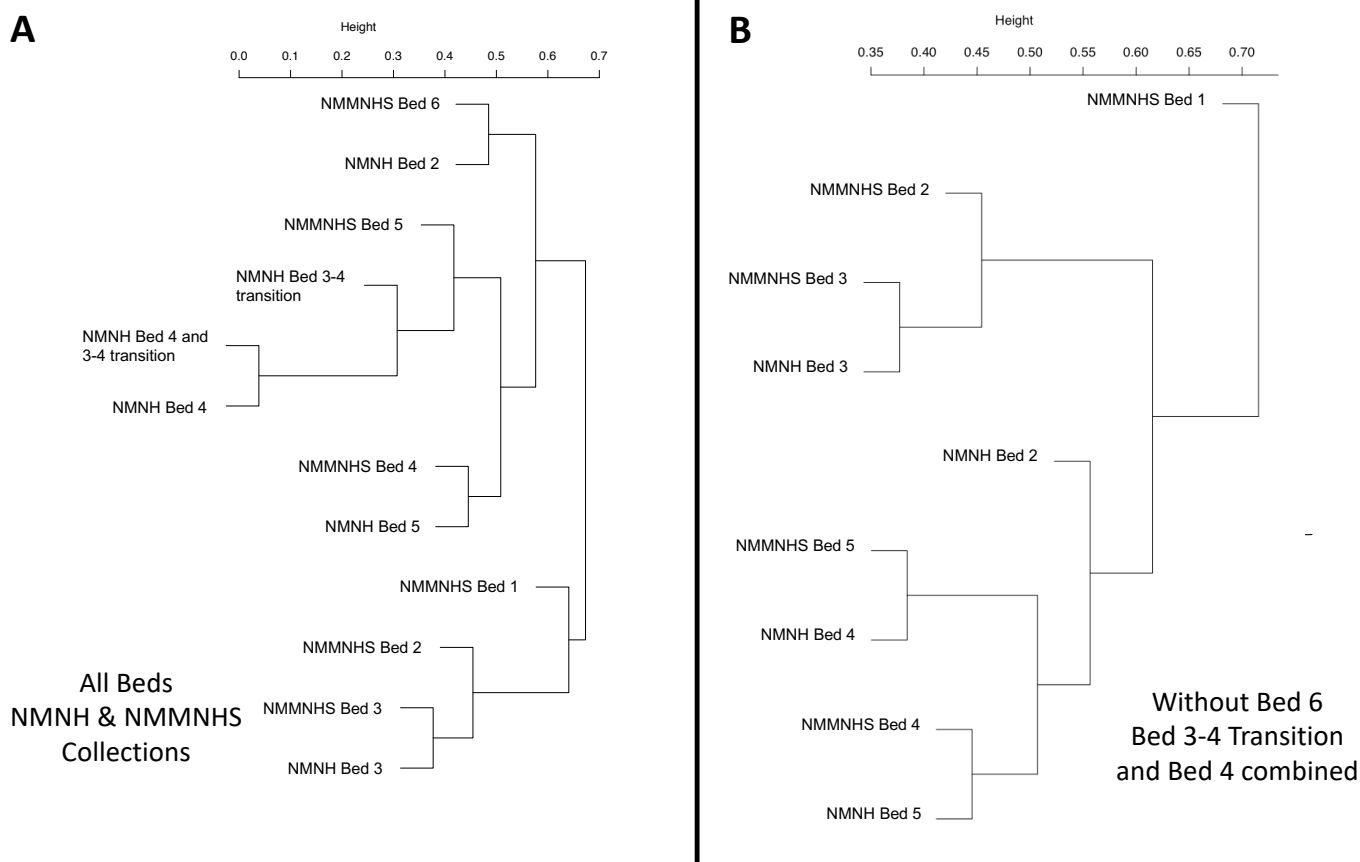


FIGURE 9. UPGMA Cluster Analysis. A. All beds from both NMNH and NMMNHS collections. B. Re-analysis with NMMNHS Bed 6 removed, and NMNH Beds 4 and 3-4 Transition combined.

DISCUSSION

The fossil-plant assemblage from Kinney Quarry is one of several well studied floras that represent seasonally dry western Pangean landscapes during the Late Pennsylvanian. The other two most notable floras are from the Missourian Garnett site, in eastern Kansas (Cridland and Morris, 1963; Winston, 1983), and the Virgilian Hamilton Quarry site, in western Kansas (Rothwell and Mapes, 1988). These three floras provide an east-to-west transect across the western part of Pangea, with Kinney as the westernmost. Garnett is of middle Missourian age and is within the Midcontinent coal measures between coal beds (Moore et al., 1936; Cridland et al., 1963; Feldman et al., 2005). It is part of a channel-fill sequence, lateral to a calcic Vertisol (Joeckel, 1989; Feldman et al., 2005) and was deposited during a seasonal climate interval between the more humid periods when peat/coal formed. The Hamilton fossiliferous deposits, shales and limestones of Virgilian age are not part of a coal-bearing sequence and appear to represent the more semi-arid part of a climate cycle. The deposit, of tidal origin, fills an estuarine channel, deposited under varying salinities (Cunningham et al., 1993). At Kinney, coal also is absent from the stratigraphic section, but the transported plant fragments in the lower beds of the sequence (Beds 1 through 6) contain a mixture of plants, some typical of Pennsylvanian wetland habitats and others more xeromorphic, considered tolerant of drought. Thus, these beds may have been deposited during the wettest parts of a glacial-interglacial cycle, but reflect the generally drier conditions of western Pangea.

Kinney may have formed in western Pangea at the same time as peat was forming in central Pangean regions during the Missourian, during the wettest part of a glacial-interglacial

cycle. The Garnett deposit, in contrast, clearly formed between times of peat formation, but in the overall wetter Midcontinent region in the western part of central Pangea. The floras of Garnett, Hamilton Quarry, and Kinney Quarry are enriched in conifers and other xeromorphic plants, with varying numbers of species typically associated with high-moisture substrates. For uncertain reasons, but perhaps related to its temporal position in the Missourian—older than both Garnett and Hamilton—Kinney has a larger representation of species that require high levels of substrate moisture than are found at the other two sites, in particular the pteridosperms *Neuropteris ovata* and several types of *Mixoneura* spp., marattialean ferns, and calamitaleans. A number of floras from New Mexico have been described recently from strata of Missourian age (Falcon-Lang et al., 2011, 2016; DiMichele et al., 2017a, b; Lucas et al., 2021); these floras, nearly all of which are of mixed composition, are significantly smaller and individually less diverse than the Kinney assemblage. These smaller floras, nonetheless, provide a geographic and temporal comparison. In addition, those of the earlier part of the Missourian are greatly enriched in xeromorphic plants and occur in sedimentary environments indicative of relatively severe periodic moisture stress (e.g., Falcon-Lang et al., 2011; Elrick et al., 2017), which appears to have been ameliorated at least locally by Kinney time.

Sample Size, Rarefaction, and Taphonomy

Sampling at Kinney has been carried out over many years, and has been somewhat opportunistic; as the quarrying moved along, different beds were exposed at different times. Field experience has led to the recognition that fossil density, diversity, fragmentation, and quality of preservation change throughout the quarry, even within any individual bed. As a consequence,

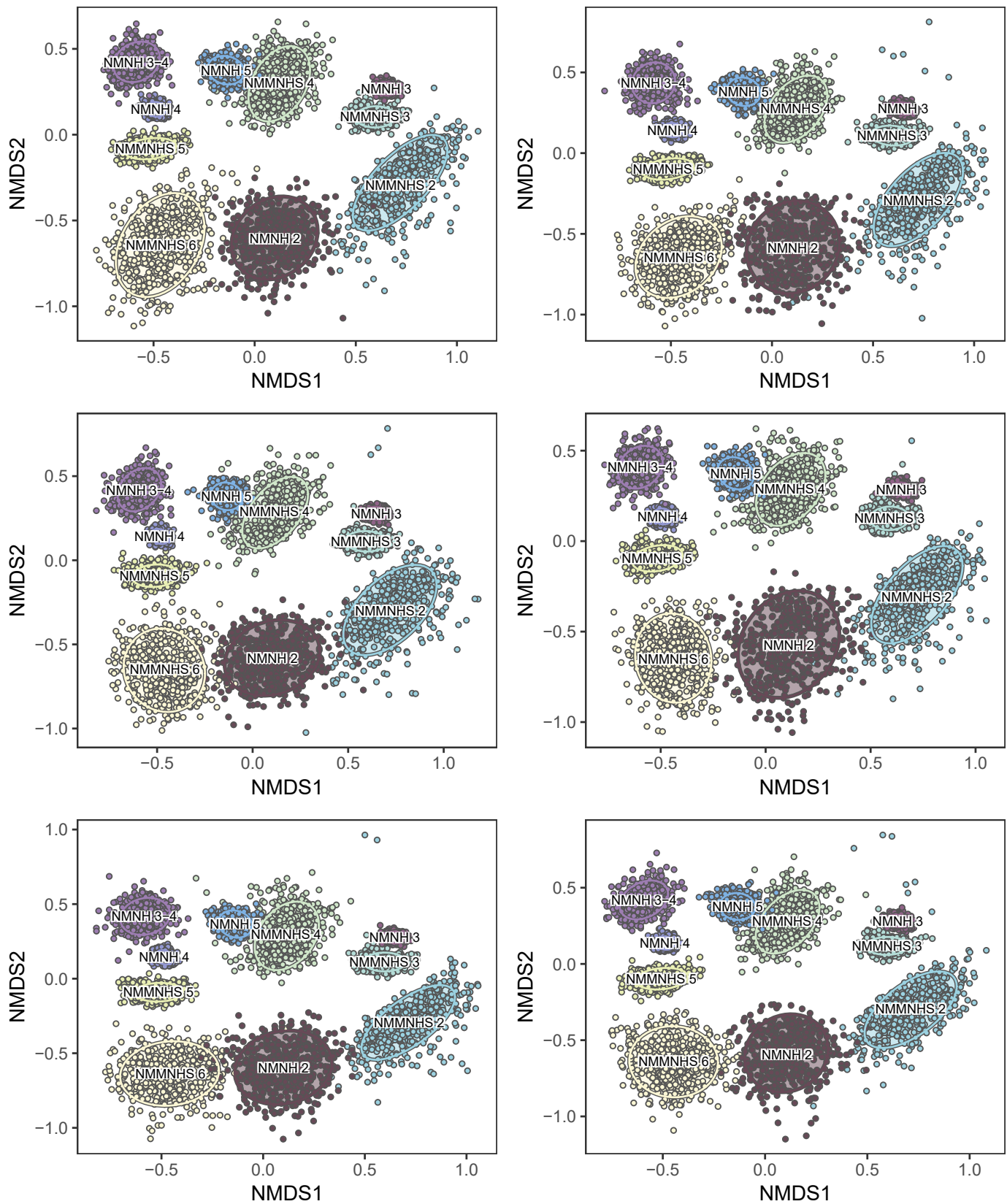


FIGURE 10. Nonmetric Multidimensional Scaling analyses of all beds, NMNH and NMMNHS collections. Each point represents one iteration of the resampling procedure. Heavy lines are 84% confidence ellipses for each bed.

the controlled excavation, although capturing temporal changes in certain aspects of composition and preservation, was still spatially constrained. However, both the NMMNHS and NMNH collections include samples made at different times, by several different collectors, which thus enhance the overall understanding of the floras.

The rarefaction analyses allow us to control for variation in sample sizes. They indicate clearly that Bed 4 contains the most diverse assemblage, by a considerable margin. This is true both for the NMMNHS and NMNH collections, the latter being the largest of the entire suite of samples (Figs. 7A and 7C). On the other hand, Beds 3 and 5 have approximately the same plant-object-type richness, with the NMMNHS and NMNH beds alternating in the four rarefaction analyses. When the NMNHS and NMNH collections are combined into a single analysis (Fig. 7D) the pattern becomes more clear, demonstrating Bed 4 to be most diverse, followed sequentially by Bed 3 and Bed 5. The Bed 2 sample is too small to yield robust diversity estimates. The combined analysis indicates that Bed 5 is approaching an asymptote, whereas Beds 3 and 4 appear to indicate still greater numbers of taxa to be found with increased sampling.

All the plant fossil accumulations are allochthonous, but the degree of allochthony may vary, as reflected in fragment size and taxonomic diversity. A more direct estimate, though, may be based on the proportion of barren surfaces. This is about the same in each collection and approaches, or even exceeds 50% (which can happen where there are part-counterpart specimens in which there are two barren surfaces out of the three). Of course, this is based only on specimens brought back from the field. Consequently, each one has some kind of specimen of interest on at least one surface, which builds-in an approximately 50% upper limit to the proportion of quadrat surfaces that are barren (possibly exceeded due to the minor complication introduced by the small number of part-counterpart specimens).

Another way to look at the nature of transport of the plant remains is to assess the degree to which any one taxon (generally represented by a single specimen) occurs alone on a given quadrat. This can be assessed by examining the summed total of individual plant-object-category frequencies. If these frequencies are converted to a proportion of total informative quadrats (Fig. 11; Table 7), they provide an index, of sorts, to the degree to which taxa tend to occur in isolation on any given hand sample. The closer the sum of percent frequencies for a given bed is to 100% (considering only informative surfaces), the closer the occurrences are to one taxon per hand sample – at exactly 100% total frequency, each quadrat would contain only a single taxonomic group. When calculated in this way, all samples average 115.3%, which means that there was not a great deal of overlap among the occurrences of plant-object categories on the quadrat surfaces. The highest total of summed frequencies is for NMNH Bed 5, which reached 146%. Plant fragment size also was largest in Bed 5, suggesting the least transport distance, and, therefore, possibly also the highest influx of plant debris, which may account for the higher overlap of fragments of different taxa on the same hand specimen. Considering the proportion of barren surfaces and the sum-total of individual frequencies together, by bed, implies that the plant fossils actually are relatively rare in the matrix. Field experience collecting material affirms that. Even though not quantified, the size of back-piles that accompany most plant excavations at Kinney (Fig. 4) and the low abundance of plant remains on the exposed surfaces, indicate that most excavated hand samples are barren on both sides, and thus not collected.

It is unexpected that Bed 5 should be the least diverse sample given its proximity to the source area, and the preservation of the largest specimens. Bed 5, with its dark matrix, large maximum and average specimen size, and relatively low diversity, might have formed quite near the shore line, and in relatively

still, shallow waters, perhaps a protected lagoon. Thus, plant-part input may have come from a restricted geographic area, primarily immediately bordering and just inland of the depositional environment. Or, this may have been caused by factors we cannot assess directly, such as alterations in the course of a nearby river that shortened transport distances, in combination with the continuing encroachment of the shoreline on the Kinney Quarry site as delta progradation proceeded.

Beds 1 and 2 are interpreted, independent of the fossil flora, as originating farthest from the shoreline but in the shallowest waters, at or even above storm wave base. Thus, the plant remains they contain should be the most allochthonous. Bed 3 is transitional, and appears to record deepening water, reflected in the presence of undisturbed, fine lamination. Only Bed 3 was analyzed for fragment size, and a greater distance from shoreline is, indeed, suggested by both the fragment-size analysis and the plant-object-category diversity of the assemblage. Just slightly more diverse than Bed 5, the assemblage of Bed 3 may have been derived from a wide area of the shoreline, from a variety of different land-surface areas and entry points. Drifting of plant remains also may have been promoted by the higher salinity and accompanying water density in the lower beds of the fill sequence. Bed 3 also would have been subject to the most open-water conditions and the effects of oxygenic decay in the water column. The latter effects may have filtered the plant-fossil content of the bed, were there to have been differential transport effects. This may be expected, especially if some types of plant remains were more prone to float than others, and if there were differential water-logging and sinking, and differential decay. In Beds 4 and 5, by contrast, the water of the embayment appears to have been progressively less saline, which would have shortened residence time of plant debris in the water column, and permitted the sinking of larger plant fragments, and even whole small plants.

We realize that Bed 5 also has low diversity. However, additional sedimentological and taphonomic evidence suggests different meanings to its low diversity compared to that of Bed 3. Unlike Bed 3, Bed 5 is from a near-shore setting, has the largest specimen sizes, and the greatest co-occurrence frequency of different taxa on hand specimens. In contrast to Bed 3, it is

TABLE 7. Summed percent-frequencies based on informative quadrats, for each bed in both New Mexico Museum of Natural History and National Museum of Natural History collections. Presented graphically in Figure 9.

Percent Informative Quadrats	
101.9	US2
103.8	NM6
104.4	US4
105.9	NM3
106.7	NM2
111.1	NM1
115.6	NM5
115.9	US3
123.5	NM4
133.6	US 3-4
145.8	US5
115.3	Average

most likely to have been affected by narrow restriction of the sources of the plant remains it preserves, and perhaps, in light of the sedimentary features of Bed 5, the most restricted and limited circulation. Thus, it would have experienced both the least mixing of source floras from the nearby land surface, and the greatest influx of plant material. Bed 5 also has thicker laminae than the other beds, which could suggest more rapid accumulation, and thus less time per unit thickness of the bed. Were this so, then lower diversity also might be a reflection of less time for natural sampling and less time averaging of the standing coastal vegetation. Finally, if the Kinney environment experienced increasing seasonality and periodic drought during the deposition of Beds 4 and 5, there might have been a real decline in the biodiversity of the site.

The real anomaly in this equation is Bed 4. The composition of the dominant elements of Bed 4, as discussed above, is not greatly different from that of Bed 5; all the samples from both the NMNH and NMMNHS are similar compositionally among the dominant elements. The diversity of Bed 4, however, at 519 quadrats, is rarefied to 53 plant-object-categories, which is about 1/4 larger than Bed 3 (n=39), and 1/3 larger than Bed 5 (n=35) at the same sample size. Yet, this bed is thought to have accumulated in a near-shore setting, under water depths and salinity similar to Bed 5. The key to understanding this may, again, lie in the size of the fragments and in the nature of the matrix. The fragment size of Bed 4 falls between that of Bed 3 and Bed 5, suggesting that although near shore, as indicated by sedimentological and stratigraphic analyses, it may have been farther offshore, in a zone of somewhat deeper water, and in an area of more active surface water flow, which would have dispersed more widely the plant material brought into this part of the sedimentary system. It also, therefore, may have been fed by a greater number of source streams, carrying a greater diversity of plant remains from the heterogeneous microhabitats on the complex, dry subhumid to semi-arid landscape (terminology of Cecil, 2003). The diversity of Bed 4, after all, is concentrated in the rare abundance categories; the most abundant elements are similar to those of Bed 5. From a lithological perspective, the lower part of Bed 4 is similar to Bed 3 in its yellow-orange iron-oxide coloring; Bed 3 is Liesegang banded, which Bed 4 is not. Bed 4 appears to consist of several facies. At least part of Bed 4 is very similar, on outcrop and in hand specimen, to Bed 5, although Bed 4 is calcareous and Bed 5 is not. The blocky facies attributed to the Bed 4 samples in the museum collections is considerably different from Bed 4 or Bed 5 in the excavation. Much of it, in both the NMNH and NMMNHS collections, is blocky and has irregular fracture, despite being laminated like excavation Beds 3 to 5. This difference in character suggests greater matrix coherence, perhaps due to greater concentration of fine grain sizes or due to its carbonate content? In any event, Bed 4 appears to have been the “sweet spot” for the mixing and accumulation of diverse elements, and may reflect a combination of plant remains transported by coastal currents and by direct river input.

Compositional Patterns in the Kinney Flora

Turning to the Kinney flora itself, systematic collection of specimens in a temporal sequence, from the bottom to the top of the beds analyzed here, reveals a clear change in composition. That change divides the deposits into two floristic groups, that of the lower three collecting beds and that of the upper three beds. The differences between these two floristic groups are largely quantitative. That is, the species pool is basically the same at all stages of the sedimentary infilling at the sample site. However, the proportions of the most frequently encountered taxa change between the Bed 1–2–3 group and the Bed 4–5–6 group.

The Bed 1–2–3 group is dominated by plants considered to be characteristic of high-moisture substrates, the pteridosperm

Neuropteris ovata, and calamitalean sphenopsids, particularly those bearing *Phyllothea*-type foliage. This latter foliage is morphologically distinctive, and its frequency in collections from this lower group of beds is as characteristic of them as is the abundance of *N. ovata*. DiMichele et al. (2013) identified *Phyllothea* sp. as *Annularia spicata*, but the morphology of the many Kinney specimens is consistent, and not in conformance with that latter species, either in the size or the shape of the foliage. It also is of interest that *Walchia piniformis* is one of the more frequently encountered plants in Bed 2 collections from both museums, but is a minor element in collections from Bed 3. This could simply be happenstance, but the replication of the pattern suggests that conifers actually are of lower abundance in Bed 3. This may reflect greater resistance of conifers to decay (see Gastaldo, 1992), although none show the indications of advanced decay and long residence in the water column described in the Gastaldo paper. Sedimentologically, the Bed 1–3 group is lithologically and genetically heterogeneous, and encompasses Facies Associations 1 and 2 of the sedimentological analysis (Schneider et al., 2020, this volume). It records the transition from limestone to clay-rich siltstone. Bed 3, in particular, which alone constituted Facies Association 2, is also described as the “fish bed” because of the relative abundance of vertebrate remains; the Bed 1–2–3 group also contains only sparse *Dunbarella*, of small size.

The pattern of similarity among the six samples that constitute the Bed 4–5–6 group is peculiar: NMNH Bed 4 is most similar, quantitatively, to NMMNHS Bed 5, and, vice versa, NMNH Bed 5 is most like NMMNHS Bed 4. This may be indicative of the spatial heterogeneity of plant fossil remains in the siltstone beds at the Kinney exposure. Clearly, the floras of these two upper beds (of the siltstone portion of the sequence) are similar, especially in the relative abundance of *Sphenopteris germanica*, even though there are other differences among them. It also is possible that some of the differences in the content of these beds reflects collection bias, particularly in USNM Bed 5. The discovery of new types of plants was the main focus of the USGS collectors, at the time the collections were made. It is quite likely that they focused on particularly productive layers and were actively over-collecting certain taxa unknown to them at the time (e.g., *Dicranophyllum readii* and *Charliea manzanitana*).

It is important to recall, at least in the way these beds have been interpreted by the stratigraphers and sedimentologists, that Bed 4 and Bed 5 were not deposited necessarily successively closer to the shoreline. In the past, both were interpreted as near-shore, shallow water deposits, of nearly fresh-water character, indicated by the large numbers of *Dunbarella* pelecypods they contain. In the present sedimentological analysis (Schneider et al., 2021, this volume), they are interpreted as having been deposited in deepening water, the result of renewed basal subsidence, and also reflecting active delta progradation. Both appear to have been sourced from relatively nearby rivers, given the increasing size of the plant remains they contain (also noted in the 2014 excavation – Schneider et al., 2021, this volume). Thus, the taphonomic conditions under which these two assemblages were deposited may have been generally similar. The distinctive Bed 4 facies found at the NMNH-USGS and NMMNHS-Huber collection sites, although very finely laminated, does not split as readily into large, plate-like, thin sheets, as do specimens from Beds 3 and 5; instead, it fractures somewhat irregularly, suggesting more matrix coherence, possibly greater clay/mudstone, or perhaps carbonate content. Furthermore, as discussed below, the Bed 4 flora is significantly more diverse than that of Bed 5, which the rarefaction analysis indicates is not a function of sample size. Thus, there may be fundamental underlying differences in the sedimentary aspects of the taphonomy of these two beds. Based on the detailed

sedimentological analysis of Schneider et al. (2021, this volume), Bed 4 still may have been receiving plant remains from coastal-parallel current transport but also increasingly from fluvial input of the prograding delta. Bed 5, on the other hand, appears to lack the coastal-transport component, and to be restricted to plant remains only from direct shoreline and nearby river input.

Bed 6 is a 0.8 m thick, olive gray siltstone with clayey layers that contain most of the fossil plants. Its flora is conifer dominated, flipping the abundances of walchian conifers and *Sphenopteris germanica* seen in Bed 5. In this pattern, it effectively extends the impression of an increase in the xeromorphic character of the vegetation in the upper beds of the sediment fill. Furthermore, Bed 6 is lithologically distinctive, yet it clusters in the UPGMA analysis (Fig. 9), with a low-level of similarity to NMNH Bed 2, and is similarly positioned in the NMDS ordination (Fig. 10), there between Bed 1–2–3 group and the Beds 4 and 5. The significance of this clustering may be questioned, given the low degree of this similarity.

Interpretation of the Kinney Floristic Patterns

The Kinney floristic analyses are in agreement with the sedimentological interpretations of the deposit (Lorenz et al., 1992; Schneider et al., 2021, this volume), which conclude that, overall, the laminated siliciclastics record a prograding deltaic

sequence, accompanied by a change in currents and in the likely source areas of the plant remains. Upsection, from Bed 1 to Bed 6, the transport distance of plant remains from the site of plant growth appears to lessen, and the source of plant remains changes from a broadly sampled coastline, possibly with many feeder streams, to a more local coastline and fewer riverine point sources. This is supported by the fragment size analysis, which indicates progressive increase in the average largest dimension of the specimens in each successive bed. The quantitative floristic composition also is congruent with the interpretation of Beds 4 and 5 as representing shoreline encroachments.

The most distinctive aspect of the flora, however, is the change in the pattern of dominance from the lower three to the upper three beds. There are several possible interpretations of the described patterns.

First is an entirely autogenic explanation in which an unchanging species pool is differentially sampled through time as physical conditions change in what became the Kinney Quarry part of a coastal embayment. In its early phases, when the lower beds formed (the basal limestone, Bed 1; the more siliciclastic-rich carbonate, Bed 2; the calcareous siltstone, Bed 3), the coastal embayment was more open to marine influence, and more distant from shoreline. The plant remains entering during this time were both transported a relatively great distance

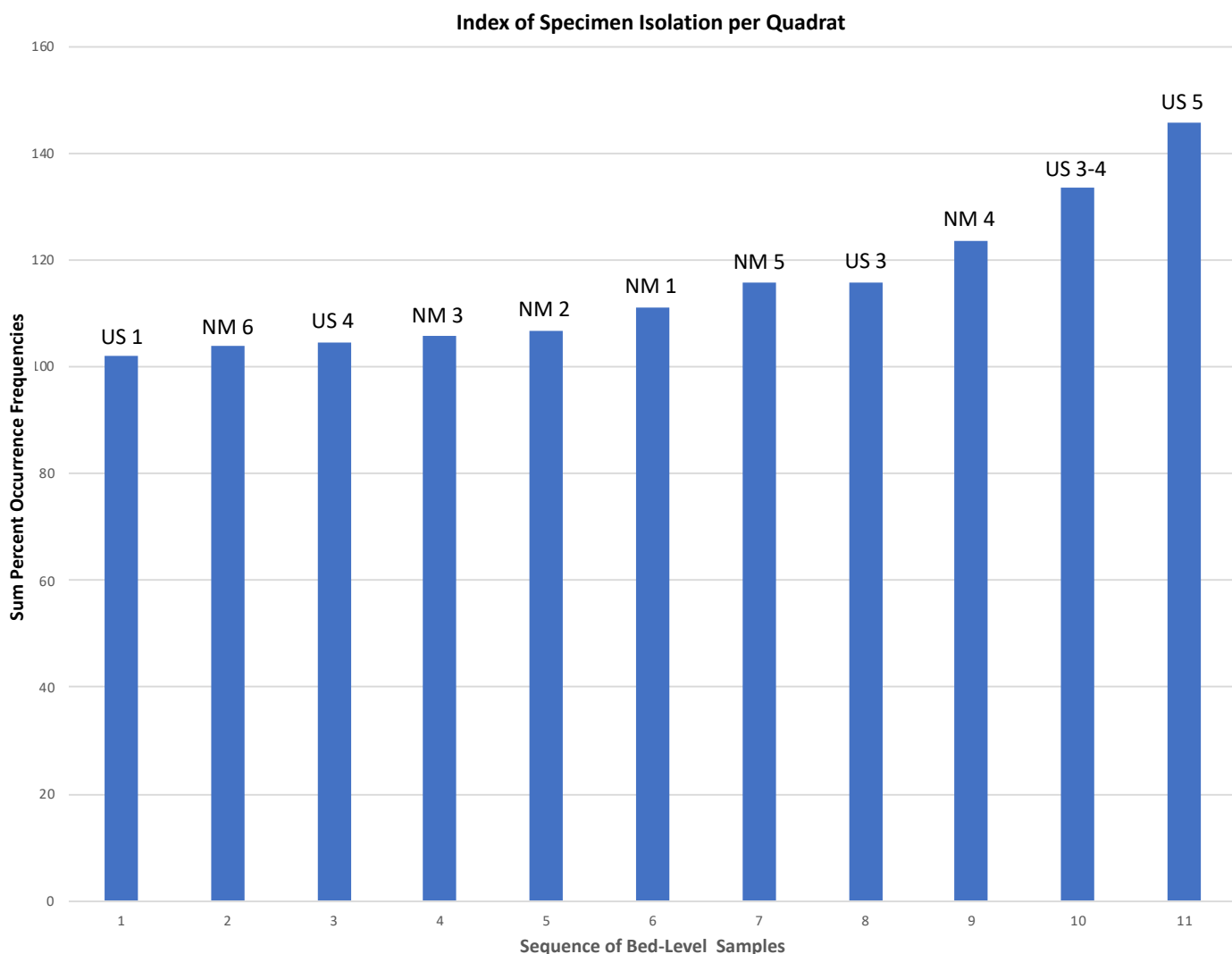


FIGURE 11. Summed occurrence frequencies, first converted to percentages of informative quadrats per bed. The closer the sum is to 100% the closer the occurrence is to one taxon per informative-quadrat surface.

and were drawn from a variety of sources, and additionally were carried and dispersed primarily by longshore currents. The embayment became more restricted, beginning with the upper parts of Bed 3 through Bed 5, as the delta increasingly prograded into the area. As this happened, the places of origin and transport dynamics of the plant remains changed. The remains in Beds 1–3 reflect longshore-current, long-distance transport, with plant remains originating from numerous entry points and a great length of coastline. Plant remains in beds 4–6 originated from fewer, more local rivers and streams and more limited reaches of coastline. Bed 4 reflects some remaining influence of longshore transport, but also reflects the increasing dominance of more local sources. This is most manifest in Bed 5, reflected in both the larger fragment size of the plant remains, as well as the increase in dominance of a few species. Such an interpretation requires that the coastal regions were dominated by xeromorphic plants, and that those less tolerant of moisture stress occupied upstream river margins, swampy areas, and feeder streams, perhaps behind the coastal fringes. As the delta prograded, and as the sources of plant remains narrowed, these coastal fringe areas, dominated by drought-tolerant, xeromorphic plants, became the main source of the local plant debris introduced into the embayment. Were wetland floras lining coastal and lower riverine habitats, they should not decrease dramatically in the upper plant-fossil-bearing beds.

Another autogenic possibility to explain the floristic change, which relies on the same physical, sedimentological interpretations, and on an unchanging regional species pool, suggests a happenstance change in the natural sampling regime of plant parts introduced to the system. Were an avulsion event, for example, to have happened upstream, it could have changed the plant communities from which litter was being derived on the nearby terrestrial landscape, thus carrying into the sedimentary system elements of a different type of vegetation, one behind the coastal and riverine fringe, and thus less commonly sampled earlier. This is congruent with high levels of habitat heterogeneity expected on a seasonally dry landscape. This explanation might account for the high diversity of Bed 4, where the effects of longshore transport still remained, carrying debris from a spectrum of sources, now mixed with the river point sources bringing in more local debris. The decrease in diversity, and increase in plant-fragment size of Bed 5, however, would then result from increasing delta progradation and a reduced source area of plant remains. It would seem, however, that drought-tolerant plants still would be required to dominate the coastal and lower riverine margins in order to account for dominance of the upper plant-fossil beds.

A third autogenic possibility suggests differential transport of the different kinds of plant remains as the driver of the vegetational change through the succession of fossiliferous beds. In this scenario, plants requiring wetter substrates are differentially transported offshore during the early phases of the succession, with a sharp change in transport patterns in the latter phases, as shoreline environments encroach. If so, progradation of the delta may have brought xeromorphic, drought-tolerant vegetation ever closer to the environment of deposition. This possibility calls for a dilution of wetland elements by an increasing input of plants from more moisture-stressed parts of the landscape. This could have a number of different causes. For example, wetland, coastal and stream/river margin taxa, typical of high-moisture substrates, must be greatly reduced in the coastal regions of the prograding delta, which was dominated by xeromorphic, drought-tolerant plants. Alternatively, the floristic changes could reflect different hydraulic properties of the plants, the xeromorphic forms being more woody in their construction, less transportable, and more prone to waterlogging, whereas wetland forms were more readily transported long distances before becoming waterlogged or being rendered unrecognizable

by decay.

A final possibility is an allogenic driver, which must be considered in light of the new assessment of a 10^3 -year time frame for accumulation of the fossil-plant bearing portion of the deposit. In this case, a change in ambient environmental conditions might cause a quantitative floristic change in the coastal region, reflected in a change in the proportions of various plant groups being introduced to the depositional environment. In the case of the Kinney succession, this change would seem to have been relatively minor, given the same basic species pool throughout the period of sediment accumulation, with some notable exceptions. Based on the vegetation alone, there being no sedimentological indication of a change in climatic seasonality, it would appear that there was some degree of increase in drought between Beds 3 and 4, continuing through Bed 6, and possibly throughout the remaining succession, given the discovery of conifer fragments in some of the higher beds.

CONCLUDING REMARKS

The Kinney Quarry fossil flora is a diverse mixture of plants, rich in forms typical of seasonally dry habitats, but with a variable, occasionally abundant, admixture of taxa generally considered to be typical of habitats with high soil moisture. The species pool is mostly consistent through the entire plant-bearing portion of the deposit, although there are changes in the patterns of dominance and diversity. The dominance of seasonally dry elements increases upward in the fill, even though the basic species pool remains the same. Changes in the dominance profiles of the six distinct beds that bear most of the plant fossils, particularly the different dominant-element distributions between the lower three beds (Beds 1–3) and the subsequent three beds (Beds 4–6), might reflect changes in taphonomic factors related to landscape compositional heterogeneity, combined with differential decay, fragmentation, transport potential, and changing proximity to the shoreline, the latter affecting the size of the land area sampled. During the time in which the Kinney deposits were forming, the paleoshoreline was moving ever closer to the present-day quarry area. Alternatively, the abruptness of the vegetational change may indicate an environmental change during the period of sediment accumulation, related to overall reduction in soil moisture, and accompanying increase in the habitat heterogeneity of the source vegetation.

The first scenario, movement of the paleoshoreline closer to the quarry location, explains the consistency of the species pool, and attributes variation in compositional dominance to physical taphonomic factors. It is an autogenic explanation, reflective of the relatively well documented changes in the taphonomic conditions. The second scenario combines these same documentable changes in transport and preservational conditions with a presumption of minor environmental changes during the time of accumulation, based on environmental tolerances of the major groups of plants. Although we cannot resolve these alternative interpretations, such contrasting explanations of the patterns observed would not have been possible without the controlled excavation, which revealed the underlying sedimentological aspects of the physical system. The controlled excavation also permitted much older, and non-oriented NMNH collections to be sorted into bed-level groups that, for the most part, correspond in lithologic character and biotic composition to those of the NMMNHS excavation.

The Kinney excavation, even more so than the studies reported by Tabor et al. (2013), Looy and Hotton (2014), or DiMichele et al. (2019), reveals that subtle changes in environmental conditions can be revealed by careful outcrop-scale, bed-level discrimination. It also demonstrates how older collections, made without reference to any small-scale stratigraphic order, can be “rejuvenated” and made more relevant by comparison with the findings of a newer, controlled

excavation. And, in comparison to the above referenced studies, the Kinney analysis shows the degree to which oriented collections document a variety of different kinds and tempos of changes on ancient landscapes, not easily understood from bulk museum collections. Carefully oriented sampling, and consideration of the underlying taphonomic factors affecting floristic composition, make it more possible to use the resulting collections to address aspects of ecosystem change and response to different rates and durations of environmental change, at time scales similar to those accessible to neocological studies. This allows interesting comparisons between modern and past systems, such as the lower diversity assemblages that characterize the late Paleozoic.

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REFERENCES

- Archer, A.W., and Clark, G.R., II, 1992, Depositional environment of the *Dunbarella* beds: An exercise in paleoecology and sediment cyclicity: New Mexico Bureau of Mines and Mineral Resources, Bulletin 138, p. 27-36.
- Bashforth, A.R. and Nelson, W.J., 2015, A Middle Pennsylvanian macrofloral assemblage from below the Rock Island (No. 1) Coal Member, Illinois: resolving the Bolsovian–Asturian boundary in the Illinois Basin: Review of Palaeobotany and Palynology, v. 222, p. 67-83.
- Boucot, A.J., Xu, C., Scotese, C.R. and Morley, R.J., 2013, Phanerozoic paleoclimate: An atlas of lithologic indicators of climate: SEPM Concepts in Sedimentology and Paleontology No. 11, 478 p.
- Clark, G.R., II, 1978, Byssate scallops in a Late Pennsylvanian lagoon: Geological Society of America, Abstracts with Programs, v. 10, p. 380.
- Cridland, A.A. and Morris, J.E., 1963, *Taeniopteris*, *Walchia* and *Dichophyllum* in the Pennsylvanian system in Kansas: University of Kansas Science Bulletin, v. 44, p. 71–85.
- Cridland, A.A., Morris, J.E. and Baxter, R.W., 1963, The Pennsylvanian plants of Kansas and their stratigraphic significance: Palaeontographica Abteilung B, v. 112, p. 58-92.
- Cunningham, C.R., Feldman, H.R., Franseen, E.K., Gastaldo, R.A., Mapes, G., Maples, C.G. and Schultze, H.P., 1993, The Upper Carboniferous Hamilton Fossil-Lagerstätte in Kansas: a valley-fill, tidally influenced deposit: Lethaia, v. 26, p. 225-236.
- DiMichele, W.A., Wagner, R.H., Bashforth, A.R. and Álvarez-Vázquez, C., 2013, An update on the flora of the Kinney Quarry of central New Mexico (Upper Pennsylvanian), its preservational and environmental significance: New Mexico Museum of Natural History and Science Bulletin 59, p. 289-325.
- DiMichele, W.A., Lucas, S.G., Looy, C.V., Kerp, H., Chaney, D.S., 2017a, Plant fossils from the Pennsylvanian–Permian transition in western Pangea, Abo Pass, New Mexico: Smithsonian Contributions to Paleobiology, v. 99, 1-40.
- DiMichele, W.A., Chaney, D.S., Lucas, S.G., Nelson, W.J., Elrick, S.D., Falcon-Lang, H.J. and Kerp, H., 2017b, Middle and Late Pennsylvanian fossil floras from Socorro County, New Mexico, U.S.A: New Mexico Museum of Natural History and Science, Bulletin 77, 25-99.
- DiMichele, W.A., Hotton, C.L., Looy, C.V. and Hook, R.W., 2019, Paleoeological and paleoenvironmental interpretation of three successive macrofloras and palynofloras from the Kola Switch locality, lower Permian (Archer City Formation, Bowie Group) of Clay County, Texas, USA. PalZ, v. 93, p. 423-451.
- Donovan, M.D., DiMichele, W.A., Lucas, S.G., and Schneider, J., 2021, Atlas of selected Kinney Quarry plant fossils, Late Pennsylvanian, Central New Mexico: New Mexico Museum of Natural History and Science Bulletin, this volume.
- Donovan, M.D. and Lucas, S.G., 2021, Insect herbivory on the Late Pennsylvanian Kinney Brick Quarry Flora, New Mexico, USA: New Mexico Museum of Natural History and Science Bulletin, this volume.
- Elrick, S.D., Nelson, W.J. and Lucas, S.G., 2017, Fossil wood from Late Pennsylvanian sabkhas in Socorro County, New Mexico: New Mexico Museum of Natural History and Science Bulletin 77, p. 101-108.
- Falcon-Lang, H.J., Jud, N.A., Nelson, W.J., DiMichele, W.A., Chaney, D.S. and Lucas, S.G., 2011, Pennsylvanian coniferopsid forests in sabkha facies reveal the nature of seasonal tropical biome: Geology, v. 39, p. 371-374.
- Falcon-Lang, H.J., Kurzawe, F. and Lucas, S.G., 2016, A Late Pennsylvanian coniferopsid forest in growth position, near Socorro, New Mexico, USA: tree systematics and palaeoclimatic significance: Review of Palaeobotany and Palynology, v. 225, p. 67-83.
- Feldman, H.R., Archer, A.W., West, R.R. and Maples, C.G., 1992, The Kinney Brick Company Quarry: preliminary analysis using an estuarine depositional model: New Mexico Bureau of Mines and Mineral Resources Bulletin 138, p. 21-26.
- Feldman, H.R., Franseen, E.K., Joeckel, R.M. and Heckel, P.H., 2005, Impact of longer-term modest climate shifts on architecture of high-frequency sequences (cyclothems), Pennsylvanian of Midcontinent USA: Journal of Sedimentary Research, v. 75, p. 350-368.
- Gastaldo, R.A., 1992, Plant taphonomic character of the late Carboniferous Hamilton Quarry, Kansas, USA: Preservational modes of walchian conifers and implied relationships for residency time in aquatic environments; in J. Kovar-Eder, ed. Palaeovegetational Development in Europe and Regions Relevant to its Palaeofloristic Evolution. Museum of Natural History Vienna, p. 393-399.
- Gotelli, N.J. and Colwell, R.K., 2011, Estimating species richness; in Magurran, A.E. and McGill, B.J., eds., Biological diversity: frontiers in measurement and assessment. Oxford University Press, p. 39-54.
- Huber, P., 1992, Faunal distribution, seasonal deposition, and fish taphonomy at the Upper Pennsylvanian (Missourian) Kinney Brick Company Quarry, central New Mexico: New Mexico Bureau of Mines and Mineral Resources, Bulletin 138, p. 37-48.
- Joeckel, R.M., 1989, Geomorphology of a Pennsylvanian land surface; pedogenesis in the Rock Lake Shale Member, southeastern Nebraska: Journal of Sedimentary Research, v. 59, p. 469-481.
- Kues, B.S., 1992a, A Late Pennsylvanian restricted-marine fauna from the Kinney Quarry, Manzanita Mountains, New Mexico: New Mexico Bureau Mines and Mineral Resources, Bulletin 138, p. 89-97.
- Kues, B.S., 1992b, The bivalve *Dunbarella* in marine and nonmarine facies of the Upper Pennsylvanian sequence at the Kinney Quarry, Manzanita Mountains, New Mexico: New Mexico Bureau of Mines and Mineral Resources, Bulletin 138, p. 99-111.
- Kues, B.S. and Lucas, S.G., 1992, Overview of Upper Pennsylvanian

- stratigraphy and paleontology, Kinney Quarry, Manzanita Mountains, New Mexico: New Mexico Bureau of Mines and Mineral Resources, Bulletin 138, p. 1-12.
- Looy, C.V. and Hottton, C.L., 2014, Spatiotemporal relationships among Late Pennsylvanian plant assemblages: Palynological evidence from the Markley Formation, west Texas, USA: Review of Palaeobotany and Palynology, v. 211, p. 10-27.
- Looy, C.V. and Duijnste, I.A.P., 2021, Three orders of branching in branch systems of late Pennsylvanian walchian conifers: New Mexico Museum of Natural History and Science, Bulletin, this volume.
- Lorenz, J.C., Smith, G.A. and Lucas, S.G., 1992, Sedimentation patterns in Pennsylvanian strata at the Kinney Brick Company Quarry, Bernalillo County, New Mexico: New Mexico Bureau of Mines and Mineral Resources, Bulletin 138, p. 13-19.
- Lucas, S.G., Allen, B.D., Krainer, K., Barrick, J., Vachard, D., Schneider, J.W., DiMichele, W.A. and Bashforth, A.R., 2011, Precise age and biostratigraphic significance of the Kinney Brick Quarry Lagerstätte, Pennsylvanian of New Mexico, USA: Stratigraphy, v. 8, p. 7-27.
- Lucas, S.G., DiMichele, W.A., Krainer, K., Barrick, J.E., Vachard, D., Donovan, M.P., Looy, C., Kerp, H., and Chaney, D.S., 2021, The Pennsylvanian System in the northern Sacramento Mountains, New Mexico, USA: stratigraphy, petrography, depositional systems, paleontology, biostratigraphy, and geologic history: Smithsonian Contributions to Paleobiology, no. 104, 215 p.
- Mamay, S.H., 1981, An unusual new species of *Dicranophyllum* Grand'Eury from the Virgilian (Upper Pennsylvanian) of New Mexico, USA: The Palaeobotanist, v. 28-29, p. 86-92.
- Mamay, S.H., 1990, *Charliea manzanitana*, n. gen., n. sp., and other enigmatic parallel-veined foliar forms from the Upper Pennsylvanian of New Mexico and Texas: American Journal of Botany, v. 77, p. 858-866.
- Mamay, S.H., 1992, *Sphenopteridium* and *Telangiospis* in a *Diplopteridium*-like association from the Virgilian (Upper Pennsylvanian) of New Mexico: American Journal of Botany, v. 79, p. 1092-1101.
- Mamay, S.H., 1994, Fossil eggs of probable piscine origin preserved on Pennsylvanian *Sphenopteridium* foliage from the Kinney Quarry, Central New Mexico: Journal of Vertebrate Paleontology, v. 14, 320-326.
- Mamay, S.H. and Mapes, G., 1992, Early Virgilian plant megafossils from the Kinney Brick Company Quarry, Manzanita Mountains, New Mexico: New Mexico Bureau of Mines and Mineral Resources, Bulletin 138, p. 61-85.
- McCune, B. and Grace, J.B., 2002, Analysis of Ecological Communities: MJM Software Design, Glenden Beach, OR, 300 p.
- Moore, A.C., Elias, M.K. and Newell, M.D., 1936, A "Permian" flora from the Pennsylvanian rocks of Kansas: Journal of Geology, v. 44, p. 1-31.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. and Wagner, H., 2018, Vegan: Community Ecology Package. R package version 2.5-2. <https://CRAN.R-project.org/package=vegan>
- Pfefferkorn, H.W., Mustafa, H. and Hass, H., 1975, Quantitative charakterisierung oberkarboner Abdruckfloren: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 150, p. 253-269.
- R Core Team, 2013, R: A language and environment for statistical computing: R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Rothwell, G.W. and Mapes, G., 1988, Vegetation of a Paleozoic conifer community; in Mapes, G. and Mapes, R.H., eds., Regional geology and paleontology of upper Paleozoic Hamilton quarry area in southeastern Kansas. Kansas Geological Survey Guidebook Series, v. 6, p. 213-223.
- Schachat, S.R., Labandeira, C.C. and Maccracken, S.A., 2018, The importance of sampling standardization for comparisons of insect herbivory in deep time: a case study from the late Palaeozoic: Royal Society Open Science, 5, 171991, <https://doi.org/10.1098/rsos.171991>.
- Schachat, S.R., Maccracken, S.A. and Labandeira, C.C. 2020, Sampling fossil floras for the study of insect herbivory: how many leaves is enough?: Mitteilungen aus dem Museum für Naturkunde in Berlin. Fossil Record, 23, 15-32, <https://doi.org/10.5194/fr-23-15-2020>.
- Sekhon, J.S., 2020, Matching: multivariate and propensity score matching with balance optimization: R package version 4.9-7. <https://CRAN.R-project.org/package=Matching>
- Schneider, J.W., Lucas, S.G., Scholze, F., Voigt, S., Marchetti, L., Klein, H., Opluštil, S., Werneburg, R., Golubev, V.K., Barrick, J.E., Nemyrovskaya, T., Ronchi, A., Day, M.O., Silantiev, V.V., Rößler, R., Saber, H., Linnemann, U., Zharinova, V., and Shen, S.Z., 2020, Late Paleozoic-early Mesozoic continental biostratigraphy – Links to the Standard Global Chronostratigraphic Scale: Paleoworld, v. 531, p. 186-238. doi.org/10.1016/j.palwor.2019.09.001
- Schneider, J.W., Legler, B., Brosig, A., Krainer, K. and Lucas S.G., 2021, Sedimentology and depositional environment of the Tinajas Member (Missourian, Late Pennsylvanian) strata in the Kinney Brick Quarry, Manzanita Mountains, Central New Mexico: New Mexico Museum of Natural History and Science Bulletin, no. 104, 215 p.
- Tabor, N.J. and Poulsen, C.J., 2008, Palaeoclimate across the Late Pennsylvanian–Early Permian tropical palaeolatitudes: a review of climate indicators, their distribution, and relation to palaeophysiographic climate factors: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 268, p. 293-310.
- Tabor, N.J., Romanchok, C.M., Looy, C.V., Hottton, C.L., DiMichele, W.A. and Chaney, D.S., 2013, Conservatism of Late Pennsylvanian vegetational patterns during short-term cyclic and long-term directional environmental change, western equatorial Pangea: Geological Society, London, Special Publications, v. 376, p. 201-234.
- Tol, P.J.J., 2019, Colour schemes and templates: URL <https://personal.sron.nl/~pault/#sec:qualitative>.
- Willard, D.A. 1992, Early Virgilian palynofloras from the Kinney Quarry, Manzanita Mountains, New Mexico: New Mexico Bureau of Mines and Mineral Resources, Bulletin 138, p. 49-60.
- Williams, S.C. and Lucas, S.G., 2013, Taphonomy and paleoecology of Pennsylvanian fishes from the Kinney Brick Quarry, New Mexico, USA: New Mexico Museum of Natural History and Science, Bulletin 59, p. 371-389.
- Winstons, R.B., 1983, A Late Pennsylvanian upland flora in Kansas: systematics and environmental implications: Review of Palaeobotany and Palynology, v. 40, p. 5-31.
- Zidek, J., ed., 1992, Geology and paleontology of the Kinney Brick Quarry, Late Pennsylvanian, central New Mexico: New Mexico Bureau of Mines and Mineral Resources, Bulletin 138, 242 p.



Artist's conception of *Elonichthys*. Artwork by Ken McKeighen.