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Plant Fossils from the Pennsylvanian–Permian Transition in Western Pangea, Abo Pass, New Mexico

*William A. DiMichele, Spencer G. Lucas,
Cindy V. Looy, Hans Kerp,
and Dan S. Chaney*

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ABSTRACT

DiMichele, William A., Spencer G. Lucas, Cindy V. Looy, Hans Kerp, and Dan S. Chaney. Plant Fossils from the Pennsylvanian–Permian Transition in Western Pangea, Abo Pass, New Mexico. *Smithsonian Contributions to Paleobiology*, number 99, viii + 40 pages, 21 figures, 1 table, 2017. — Plant fossils are described from five stratigraphic levels spanning the Pennsylvanian–Permian boundary in Abo Canyon, New Mexico. Charles B. Read collected the fossils in 1940 and 1941; Read's field notes cannot be located. A combination of Read's bed numbering pattern, his notes in the collections, and collection taxonomic composition permits them to be placed in an oldest to youngest sequence. The youngest fossils, from the Abo Formation of early Permian age, anchor the collection stratigraphically. A collection labeled "Base of Red Magdalena" is most likely equivalent to the modern Bursum Formation, thus immediately below the Abo. The three remaining collections are from the Upper Pennsylvanian portion of the Atrasado Formation. All collections are dominated or codominated by plants typical of environments with seasonal moisture stress and record increasing moisture limitation through time. Conifers, *Sphenopteris germanica*, and mixoneurid odontopterids are common to abundant in pre–Abo Formation collections. These same collections also contain wet-substrate taxa, particularly calamitaleans and marattialean tree ferns, with arborescent lycopsids in the oldest collection. The middle three collections contain the remains of microconchids/spirorbids, snails, ostracods, and conchostracans closely associated with the plant remains, indicating brackish to marine salinities at the burial sites of the organics. The Abo Pass collections document Pennsylvanian–Permian floristic changes in the western Pangean equatorial belt, an important point of comparison to better studied floras from this same interval in central Pangea (eastern United States and Europe). Most of the plants in the western equatorial assemblages are the same as those of similar age from west central to central Pangea (Euramerica), indicating a widespread tropical biogeographic province at this time, but within which there were several distinct biomes.

Cover images, from left to right: Selected details from Figures 12e, 16h, and 9g.

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Plant Fossils from the Pennsylvanian–Permian Transition in Western Pangea, Abo Pass, New Mexico

William A. DiMichele,^{1} Spencer G. Lucas,² Cindy V. Looy,³
Hans Kerp,⁴ and Dan S. Chaney¹*

INTRODUCTION

The Pennsylvanian–Permian transition encompassed a gradual global environmental change that, on average, involved the shift from a wetter Pennsylvanian to a drier Permian. This transition was, however, complex in its expression, varying geographically in timing, intensity, and details, not happening at all in parts of eastern Pangea, namely, present-day China (e.g., compare the patterns in western Pangea [Montañez et al., 2007; Tabor and Poulsen, 2008; Tabor et al., 2013], west central Pangea [Blake and Gillespie, 2011; Cecil, 2013; Montañez and Cecil, 2013], east central Pangea [Roscher and Schneider, 2006; Opluštil and Cleal, 2007; Cleal et al., 2012], and eastern Pangea [Hilton and Cleal, 2007]). Superimposed on this transition were glacial-interglacial cycles of the late Paleozoic ice age, which encompassed all of the Pennsylvanian and much of the early Permian (Cecil, 1990; Fielding et al., 2008; Montañez and Poulsen, 2013; Cecil et al., 2014). Furthermore, because of the gradual and areally variable nature of the environmental changes, the boundary between the Pennsylvanian and Permian is not marked by a major geological hiatus (Cecil, 2013). As a result, the placement of the boundary has been difficult and controversial, particularly in terrestrial sections, both in the means used to identify it and in the reliability with which it can be identified in different places throughout the world.

In New Mexico, this transition is exposed throughout the central part of the state from its southern reaches near Alamogordo, through the central portion of the state east of Socorro, and into Abo Pass (Figure 1). Although studies of the regional geological and paleontological aspects of this transition have been published (e.g., Read and Wood, 1947; Lucas et al., 2013), a detailed synthesis of the paleobotanical changes in this important region of western Pangea remains incomplete. A general overview of the changes was provided by Ash and Tidwell (1982) and remains a good summary of the basic patterns.

We report here on plant-fossil collections from five stratigraphic levels in Abo Pass (Figure 1) made principally by Charles B. Read in 1940, and supplemented in 1941, in his capacity as a paleobotanist and field geologist for the U.S. Geological Survey (USGS). The specimens are housed permanently in the collections of the National Museum of Natural History in Washington, D.C. Unfortunately, as will be discussed below, the disposition of the field notebooks associated with these collections is not known, forcing us to rely on secondary sources to assess the stratigraphic interval covered by the

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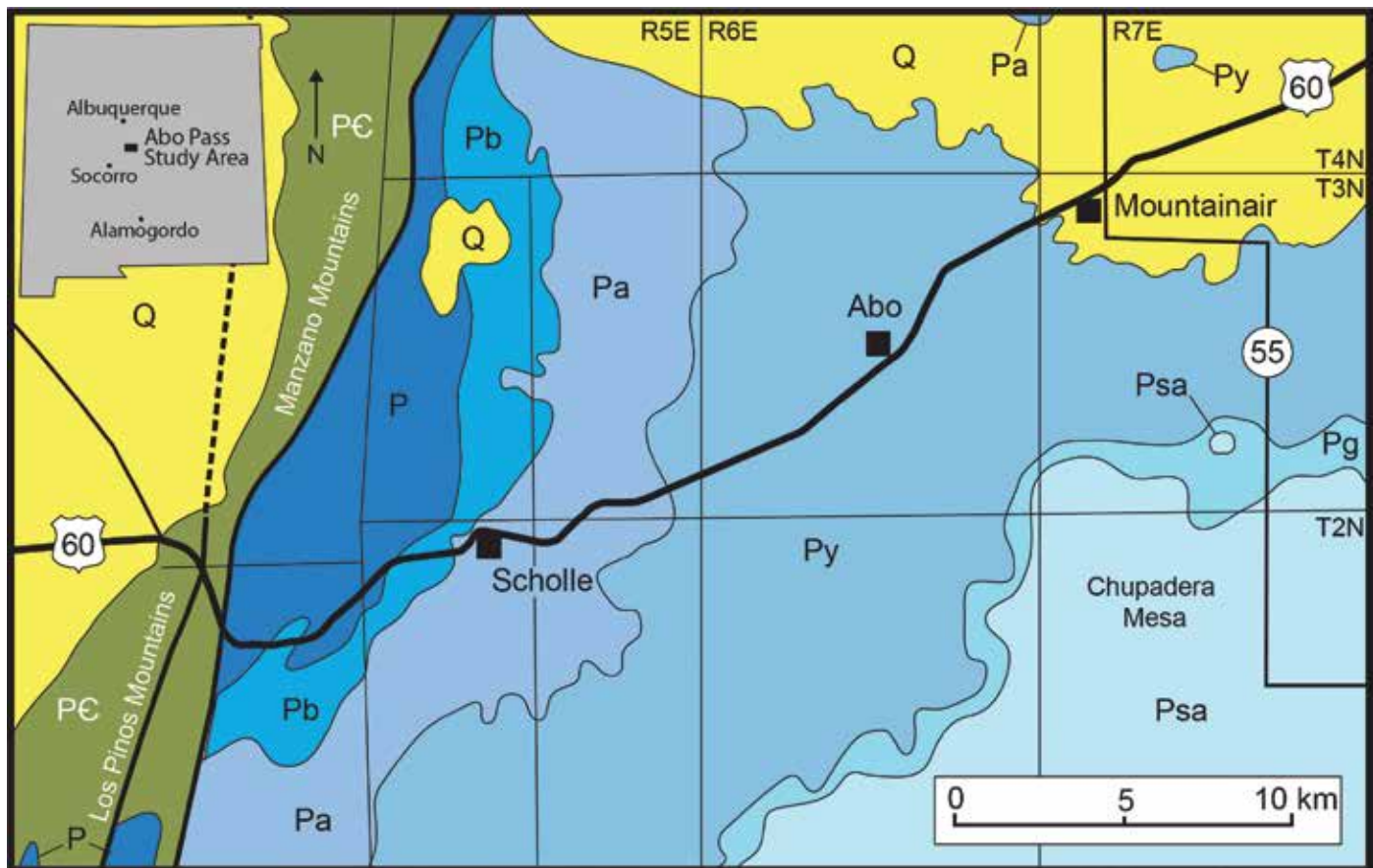


FIGURE 1. Location of the study section in Abo Pass, New Mexico. According to Read and Wood (1947), the study was carried out in Townships 2N and 3N, Ranges 5E and 6E. P = Pennsylvanian, Pa = Abo Formation, Pb = Bursum Formation, PC = Precambrian, Pg = Glorieta Sandstone, Psa = San Andres Formation, Py = Yeso Group, and Q = Quaternary.

collections. The fossil assemblages compare most closely with those described from the Pennsylvanian–Permian boundary elsewhere in Euramerica, including the Dunkard of the U.S. Appalachian Basin (Blake and Gillespie, 2011), Rotliegend of Germany (e.g., Potonié, 1893; Barthel, 1976, 2009; Kerp and Fichter, 1985; Barthel and Brauner, 2015), the Autunian of France (e.g., Zeiller, 1890, 1892, 1898, 1906; Doubinger, 1956; Galtier and Broutin, 1995, 2008; Steyer et al., 2000; Bercovici and Broutin, 2008), and other European strata that encompass the Pennsylvanian–Permian transition (e.g., Broutin, 1981; van Amerom et al., 1993; Wagner and Martínez García, 1982; Popa, 1999; Šimůnek and Martínek, 2009).

GEOLOGY

Read measured his stratigraphic section in Abo Canyon (Figure 1) in the “southeastern part of Casa Colorado Grant, and portions

of T. 2 and 3 N., R. 5 and 6 E., between Sais Quarry and Abo State Monument, Socorro and Torrance Counties, New Mexico” (Read and Wood, 1947). At the time, the Sais Quarry (or crusher) was on the western end of the measured section, a site where ballast was quarried and crushed for use by the railroad—this quarry ceased operations in the 1950s. The Abo State Monument, on the eastern end, refers to the Abo ruins. The study area is on the USGS Scholle and Abo 7½ minute quadrangles. Read most likely investigated exposures along the railroad, along U.S. Highway 60, which parallels the railroad for much of its traverse through Abo Canyon, and in side canyons along this route. There are many canyons branching off to the north and south of the railroad, and active copper mining occurred in that same area from beds in the Abo Formation (Hatchell et al., 1982).

We do not have Read’s field notes, and they have not been located in either the archives of the U.S. Geological Survey in Denver or in the U.S. National Archives in Beltsville, Maryland; the latter holds a large collection of microfiche created by the

USGS from paper copies of notebooks they hold. Lacking the field notes, we also lack the details of the measured section, which, of course, is a serious handicap to understanding the stratigraphic positions of the fossil plant collections subsequently described. An Abo Canyon section was published in 1944 by Read et al. and again in 1947 by Read and Wood (their fig. 4, columnar section 13; reproduced as part of Figure 2 of this work) but in each instance in only a general way, as part of a larger study, and at a scale that precludes clearly identifying likely source beds.

Nonetheless, the plants themselves point to the general part of the section from which they were derived, most bearing strong similarities to floras from European sites from the Late Pennsylvanian to the Pennsylvanian–Permian transition. Thus, the majority of the collections are likely from either the Bursum Formation and/or the “upper, arkosic member of the Madera Limestone” (Atrasado Formation; cf. Lucas et al., 2014). According to the Read and Wood (1947) section, the Bursum Formation is about 35 m thick, and the arkosic member of the Madera Limestone is approximately 125 m in thickness in the measured section. More siliciclastic beds are noted in the arkosic member of the Madera Limestone than in the Bursum.

From an age standpoint, the youngest strata from which Read and colleagues collected plant fossils were of the Abo Formation, which is lower Permian, spanning the middle to upper Wolfcampian and lowermost Leonardian, in regional U.S. chronostratigraphic terminology. These stages are the equivalent of the Asselian through the lower Kungurian in international terms (Lucas et al., 2005, 2015). Although Read numbered the beds in the 1940 section, no bed number was assigned to the collections from the Abo. The rest of the collection comes from four beds, identified as Unit 8, Unit 10, Unit 35, and Base of Red Magdalena. The plant-fossil content suggests that the lower numbers are from near the top of the section, possibly beginning in the Bursum Formation, and that the Red Magdalena, collected in 1941, also may be from the Bursum Formation. The Pennsylvanian–Permian boundary lies either within or at the base of the Bursum Formation, depending on which marine index fossil is chosen to mark the base (see Lucas et al., 2016, for discussion). The Madera Limestone is equivalent to the Gray Mesa (lower gray member) and Atrasado (upper arkosic member) formations, according to the graphic correlation of Read and Wood (1947) (Figure 2). The lower gray member encompasses most of the Desmoinesian (upper Middle Pennsylvanian), whereas the upper arkosic member spans the upper Desmoinesian, Missourian (lower Upper Pennsylvanian), and Virgilian (Upper Pennsylvanian) U.S. regional stages, approximately equivalent to the upper Moscovian, Kasimovian, and Gzhelian, respectively, in international terms (Lucas et al., 2013).

Some attributes of the depositional environments in which the floras are preserved can be deduced from the lithological characteristics of the rock matrices in which they are preserved. Basic grain size; sedimentary structures (lamination, various kinds and degrees of cross bedding); the disposition of the

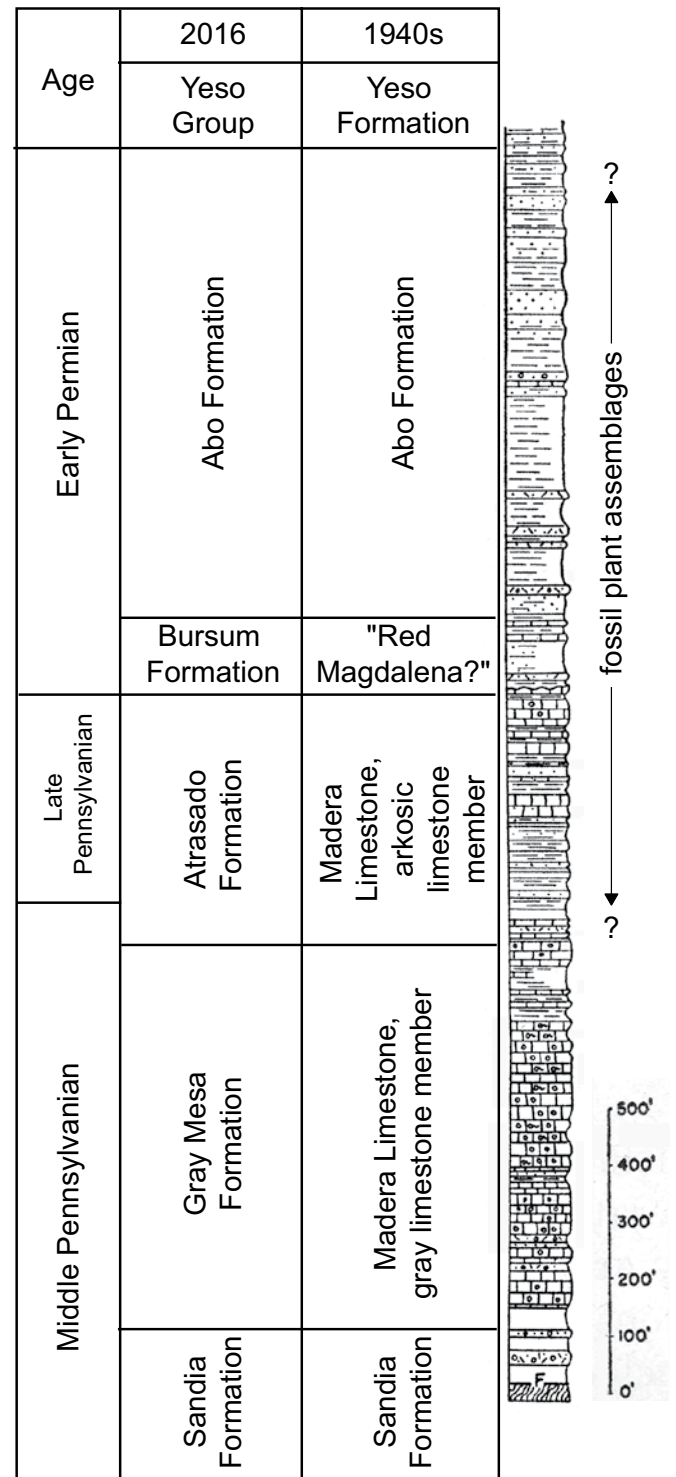


FIGURE 2. Geological section in Abo Pass (see text for details). Plant fossils come from the Abo Formation and from several levels in the Bursum and Atrasado formations. Geological column is from Read and Wood (1947, fig. 4) in *Journal of Geology*, used with permission of The University of Chicago Press.

plants in the matrix (Are they flat lying? Do they cross bedding planes? Are they folded and twisted?); the presence of comminuted plant debris (CPD); its relative abundance and distribution; and the distribution and abundance of such sedimentary particles as muscovite all assist in determining the degree of energy in the system at the time plant parts were deposited. Animal remains associated with the plants also provide insights into relative salinity and the amount of water table or shoreline fluctuation. However, the lack of data on outcrop-scale interpretations of the sedimentary environments is a significant handicap. As will be seen from discussions of each flora, the environmental conditions under which they were deposited, to the degree we can determine them, vary from little to significantly different, indicating that whereas all may have been deposited under seasonal climatic regimes, the position of the depositional environment relative to the coastline and the specific environment in which deposition took place vary among the collections. Hence, comparisons of them cannot be considered “isotaphonomic” (Behrensmeyer et al., 2000) at the level of the depositional environment.

METHODS OF ANALYSIS

Each collection was examined primarily at hand-lens magnifications of $\times 3$, $\times 4$, and $\times 7$, with microscopic examination supplemented where necessary. Photography and subsequent enlargement and image enhancement permitted recognition of features in especially difficult specimens.

The plant remains in all collections but those from the Abo Formation are fragmentary, often of quite small size. As a consequence, identification of many of these remains was difficult, and multiple possibilities often exist for their natural affinities. The identification possibilities were narrowed by comparing the New Mexico material mainly with floras or monographic works encompassing Upper Pennsylvanian and Pennsylvanian–Permian boundary strata, which are the most likely points of comparison based on lithostratigraphic and marine invertebrate biostratigraphic assessments of the age of the strata in the collection area. The authors realize these comparisons place biases on the scope of the search for similar forms, but they also facilitate identification within the limited time frame permitted for this study.

Quantitative assessments of each flora were carried out using a modification of the hand-sample/quadrat method of Pfefferkorn et al. (1975), as described by Bashforth and Nelson (2015). In this method, top and bottom surfaces of each hand sample are treated as separate sampling quadrats. All plant taxa occurring on a surface are noted as *present* and recorded only once, regardless of how many individual specimens of that taxon may be present. Barren surfaces are noted and compiled. Part and counterpart faces, if present, were treated as the same surface and counted only once. This type of analysis addresses the problem of what to count in undertaking a quantitative analysis, with the underlying presumption that estimation of biomass is

the primary objective of the quantification. It accounts for the fact that many specimens may be highly fragmented into small pieces, whereas others, which may account for significantly more biomass than all the small material combined, may be represented only by large, intact, single specimens.

This kind of quantification yields a frequency of occurrence of each category counted (taxa or objects, such as axes) compared to the total number of quadrats (hand samples analyzed). Reported frequencies of occurrence are calculated only as a percentage of the total fossiliferous quadrats, with part and counterpart surfaces counted only once; barren surfaces are not considered in the calculation of the total number of quadrats. Therefore, the reported percentages given for all categories below may add up to more or less than 100% because the occurrence frequencies of each taxon are independent measurements (there is no closure, unlike with absolute count measurements).

Animal remains were noted, and their occurrences were tabulated in a manner similar to that of the plants. However, if only animal remains were present, such quadrats were tabulated as barren with regard to further analysis of plant occurrence frequency.

The results of the quantitative analysis are presented in Table 1. These are the actual occurrence data for the categories of identifiable material (mainly taxonomic groups) in the collection. It is important to remember that these are frequency data reflecting the number of quadrats (hand-sample surfaces) on which a category was identified, not category counts. Consequently, they are nonadditive within any given collection because more than one category may occur on any given quadrat surface.

A NOTE ON CONIFER TAXONOMY

Conifers dominate or occur at high frequencies in all the collections analyzed in this study. These remains have been classified as *morphotypes*, following the procedures and character analysis used by Looy and Duijnste (2013), rather than being assigned to genera or species. We believe all these plants to be walthian conifers. The reader familiar with them will note morphologies similar to such taxa as *Ernestiodendron* (Morphotype A), *Walchia piniformis* (Morphotype B), and *Walchia schneideri* (Morphotype D). Morphotype C, represented by few specimens, has more orders of branching and different leaf angles than the other forms and appears to be a previously unrecognized form that may not fit into a described species. Detailed analysis suggests that the New Mexico material differs in subtle but consistent ways from the type concepts for these described, aforementioned taxa.

ABO FORMATION

Two collections were made by Charles B. Read from strata of the Abo Formation in Abo Canyon, USGS localities 8952, in June 1941 (based on USGS collections catalog), and 8977, undated but which we presume to have been made in July of 1940

TABLE 1. Results of quantitative analysis (see text for details). Localities are in presumed stratigraphic order from left to right, youngest (Abo Fm = Abo Formation) to oldest (Unit 35). For Abo Formation collections, counting quadrat occurrences was not practicable; X = present. *Walchia* sp., mixoneurid *Odontopteris*, and marattialean foliage nonspecific are cumulative categories. Where numbers of quadrat occurrences are given, subdivision by morphotype or species was not carried out during the quantification. Morphotypes or species identified as PND = present but not differentiated during quantitative analysis. For the marattialean foliage nonspecific category in Unit 35, several morphotypes were present, but only one was identified, marked by PND. A long dash (—) = absent from the collection; NA = not applicable.

Category or result of analysis	Locality				
	Abo Fm	Red Magdalena	Unit 8	Unit 10	Unit 35
Total quadrats	NA	81	95	269	101
Total barren surfaces	NA	46	45	115	52
<i>Supaia</i> sp.	X	—	—	—	—
<i>Walchia</i> sp.	X	—	12	—	18
<i>Walchia</i> Morphotype A	—	18	PND	32	—
<i>Walchia</i> Morphotype B	—	49	PND	152	PND
<i>Walchia</i> Morphotype C	—	2	—	—	—
<i>Walchia</i> Morphotype D	—	3	—	7	PND
Conifer cones bract scales	—	1	—	9	6
<i>Cordaitea</i>	—	1	6	10	—
<i>Sphenopteris germanica</i>	—	—	25	6	12
<i>Taeniopteris</i>	—	2	—	—	—
<i>Autunia naumanii</i>	—	—	—	—	1
<i>Autunia conferta</i>	X	—	—	—	—
<i>Rhachiphyllum</i> sp.	—	4	—	1	—
cf. <i>Peltaspermum</i> sp.	—	1	—	2	—
cf. <i>Peltasperm</i> pollen organs	—	—	—	1	—
Mixoneurid <i>Odontopteris</i>	—	—	16	16	—
<i>Odontopteris</i> (<i>Mixoneura</i>) <i>schlotheimii</i>	—	8	PND	PND	3
<i>Odontopteris</i> (<i>Mixoneura</i>) <i>subcrenulata</i>	—	—	PND	PND	5
<i>Odontopteris brardii</i>	—	—	—	—	10
<i>Reticulopteris</i> sp.	—	—	—	15	—
<i>Alethopteris schneideri</i>	—	—	—	3	—
<i>Alethopteris virginiana</i>	—	—	—	—	1
<i>Macroneuropteris scheuchzeri</i>	—	—	—	—	18
<i>Pseudomariopteris cordato-ovata</i>	—	—	—	—	1
Neuropterids	—	3	—	15	15
Marattialean foliage nonspecific	—	—	—	—	14
<i>Pecopteris densifolia</i>	—	—	—	2	—
<i>Polymorphopteris polymorpha</i>	—	—	—	—	PND
<i>Lobatopteris geinitzii</i>	—	—	—	2	—
<i>Oligocarpia gutbieri</i>	—	—	—	6	5
<i>Sphenopteris matheti</i>	—	—	—	1	1
<i>Sphenopteris</i> spp. (ferns)	—	—	2	—	1
<i>Charliea</i> sp.	—	—	—	1	—

(Continued)

TABLE 1. (Continued)

Category or result of analysis	Locality				
	Abo Fm	Red Magdalena	Unit 8	Unit 10	Unit 35
Calamitalean stems	—	1	8	3	10
<i>Annularia spicata</i>	—	—	1	2	8
<i>Annularia carinata</i>	—	—	—	—	1
<i>Annularia</i> spp.	—	3	—	—	—
<i>Calamostachys spicata</i>	—	—	—	1	—
<i>Sphenophyllum gilmorei</i>	X	—	—	—	—
<i>Sphenophyllum thonii</i>	—	—	—	2	—
<i>Sphenophyllum oblongifolium</i>	—	—	—	—	12
<i>Sphenophyllum</i> spp.	—	—	2	1	6
<i>Lepidostrobohyllum hastatum</i>	—	—	—	—	3
<i>Lepidophylloides</i> sp.	—	—	—	—	2
Small lycopsid axes	—	—	—	—	3
Striate axes	—	6	15	25	71
Woody axes	—	2	27	10	—
Seeds	—	2	9	51	10
Comminuted plant debris	—	5	—	68	26
Roots	—	—	—	—	12
Charcoal	—	—	—	1	1
Conchostracans	—	—	14	—	—
Microconchids	—	17	—	10	—
Ostracods	—	6	15	2	—
Snails	—	1	—	8	—
Linguloids	—	—	1	—	—

(on the basis of the noted presence of his field partner for that year, H. W. Ervin, who is credited on other collections made at that time in Abo Canyon). We made two additional collections in 2000 and 2001 as U.S. National Museum (USNM) localities 41672 and 41873.

Three of the four total Abo sites (USGS and USNM) can be confidently located near the Scholle railroad siding on U.S. Highway 60. Collection USGS 8977 is noted only as being made “at Scholle” by C. B. Read (note in collection drawer). Collection USNM 41672 is from Cañon Saladito on the south side of the highway, and USNM 41873 is from Cañon Salado on the north side of the highway. We suspect that the location of USGS 8952 is close to or identical to that of USNM 41873 on the basis of its lithology and fossil content, which are almost identical, including the presence of the unusual species *Sphenophyllum gilmorei*, which we have not found at any other of dozens of Abo collecting sites.

AGE AND DEPOSITIONAL ENVIRONMENT

The Abo Formation in Abo Canyon is of early Permian age. In central New Mexico, the Abo Formation, which is time transgressive from south to north in the state, may be as young as Artinskian, in international terminology, and encompasses the middle to upper part of the Wolfcampian and lower Leonardian (Lucas et al., 2005, 2015). The Abo collections reported herein are thus the youngest of the specimen suite collected by Read. The lithologies of the specimens that make up all four of these collections are similar and typical of many fossiliferous exposures in the Abo Formation throughout southern and central New Mexico. They consist of siltstone to fine-grained sandstone of pinkish red color. Specimens, many of which are large and exceed hand-sample size and may be >10 cm thick, are mostly massive to irregularly laminated. Collection USNM 41672 was noted in the field to be a fine-grained sandstone with weak

indications of trough cross bedding. Plants were abundant in float and were found in place at the top of a low bluff. The plants appeared to have been confined to the channel facies, which was scoured into purple mottled paleosols. Consistent with entombment during active sediment transport, the plants in all four collections include many specimens that are disposed at different angles in the rock matrix, often at odds with one another, suggesting rapid burial and high rates of sediment deposition.

FOSSIL FLORA

No quantitative assessment of fossil taxonomic content was made for the Abo collections. All are or appear to have been from float and thus are not necessarily reliable indicators of the proportional composition of the flora. Additionally, we did not make, and there are no indications that Read made, any quantitative assessments of floral composition in the field. Experience has shown that the best way to quantify Abo floras is on site, from large float or well-exposed bedding surfaces, because of, first, the difficulty of digging specimens out of the hard siltstone-sandstone matrix and, second, the often sparse occurrences of fossils at any given location.

Collections USGS 8952 and USNM 41873 consist of mixed floras, and as mentioned above, the floral composition, including the presence of *Sphenophyllum gilmorei*, and the similarities in color, texture, and bedding characteristics of the two deposits suggest possible derivation from the same beds.

The flora includes the following taxa:

- walchian conifers, possibly of more than one species (Figure 3a)
- the sphenopsid *Sphenophyllum gilmorei*, an unusual and rarely reported species of groundcover sphenopsid (Figure 3b,c), originally described by White (1929) from the Supai Formation (lower Permian) of the Grand Canyon, Arizona
- a single specimen of what is possibly the peltasperm *Autunia conferta* (Figure 3d), encountered at USNM 41873
- the peltasperm *Supaia thinnfeldioides* (Figure 4d)

White (1929), in his original description of *Supaia*, created many species, all which may be morphological variants of a single species, which we treat here as *S. thinnfeldioides* (see DiMichele et al., 2007, for discussion).

Hatchell et al. (1982) also reported and illustrated plants from Abo Canyon in the vicinity of Scholle, from Cañon Salado, likely in the same general area as USNM 41873 and USGS 8952. Their flora consists of *Supaia thinnfeldioides* and two morphotaxa of walchian conifers; callipterids also are referenced but not illustrated. Thus, this flora also is similar in its mixed composition to the USGS and USNM floras from this location; C. B. Read is credited with plant identifications.

Collections USGS 8977 and USNM 41672 consist entirely of *Supaia thinnfeldioides* (Figure 4a–c). Such monospecific composition is typical of the Abo Formation throughout its extent (DiMichele et al., 2013a). The dominant Abo elements at most sites are walchian conifers, and these appear to have been abundant across the Abo landscape. However, *Supaia*, the second most common element of the Abo Formation, is locally abundant and occurs most commonly in monospecific accumulations or with only rare walchian conifer specimens. *Supaia* may have been a small, streamside plant that tolerated flood disturbance and tended to grow in dense stands (DiMichele et al., 2012). Although the Abo flora is relatively diverse, all other elements are rare.

BASE OF RED MAGDALENA

A collection identified as originating at the “base of the Red Magdalena” is USGS locality 8951. This collection was made in 1941, but a note in the collection drawer says “see coll. of 1940.” The absence of a bed number is surprising, given this note, so it is possible that the note refers to a collection since lost or that the fossiliferous bed was identified in 1940 but was collected intensively only during a return visit in 1941. The combined flora and lithological matrix of this collection are not similar to any of the others described below, however, suggesting a distinct fossiliferous bed.

The term *Red Magdalena* does not hold any formal stratigraphic significance, although it was used informally in the early to mid-twentieth century. We believe that it most likely refers to strata of the Bursum Formation. Read and Wood (1947) specifically refer the Pennsylvanian strata throughout central New Mexico to the Magdalena Group and note the more terrestrial and more oxidized (= red) nature of the younger units. Thus, it is possible that the Red Magdalena is from the upper parts of the Magdalena Group, hence the Bursum Formation. In this case, USGS 8951 is not the stratigraphically lowest collection made by Read in Abo Canyon (that most likely being Unit 35). Although its position relative to the other beds remains uncertain, the lack of a bed number and a probable Bursum affinity lead us to place 8951 below the Abo Formation at this time.

In the Red Magdalena collection, plant fossils are preserved in a buff siltstone with blocky fracture. Although bedding or lamination is not prominent, the plant fossils are horizontally disposed, suggesting that bedding surfaces are present, and some surfaces are covered with small muscovite flakes. Comminuted plant debris is rare, and plant fossils vary in size from small fragments to occasional pieces of larger branches. No charcoal was noted. Animal fossils are common and consist of spirorbirds/microconchids, ostracods, and small snails (Figure 5a,c). The spirorbirds heavily encrust coniferous plant remains. Overall, the nature of the matrix and the animal remains suggest a freshwater to brackish-water coastal environment, perhaps a quiet embayment (e.g., Taylor and Vinn, 2006; Bennett, 2008).

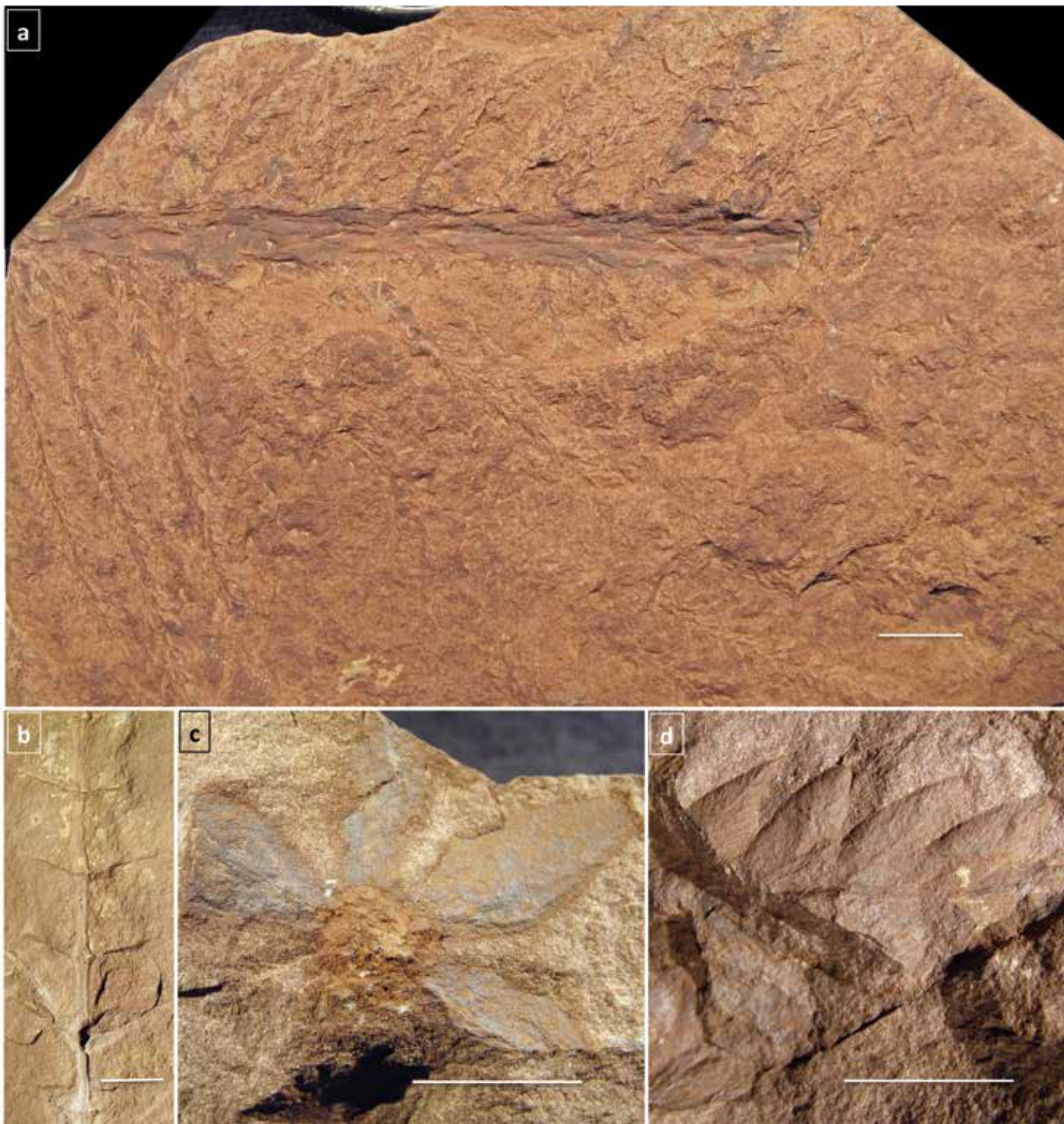


FIGURE 3. Abo Formation flora. (a) Walchian conifer, USNM specimen 618975, USNM locality 41873. (b) Longitudinal section through a cast of the small sphenopsid, *Sphenophyllum gilmorei*. USNM specimen 618977, USNM locality 41873. (c) A whorl of *Sphenophyllum gilmorei* leaves showing typical obovate shape with greatest width in the lower $\frac{1}{3}$ of the leaf and tapering apex. USNM specimen 618978, USGS locality 8952. (d) Possibly *Autunia conferta*, with vaulted pinnule lamina, well-developed pinnule midribs, and steeply ascending, relatively straight pinnule lateral veins. USNM specimen 618976, USNM locality 41873. Scale bars = 1 cm.

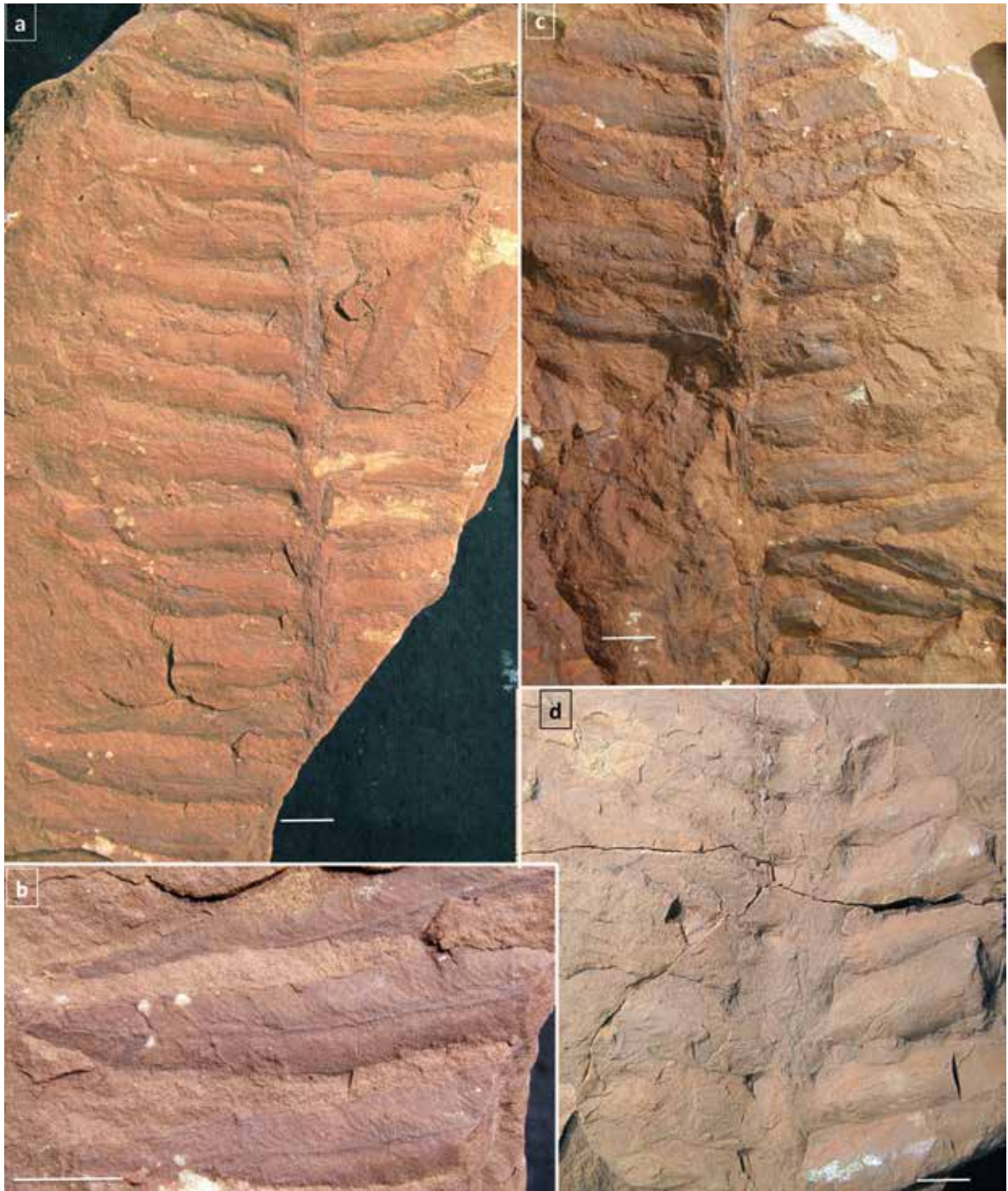


FIGURE 4. Abo Formation flora: *Supaia thinnfeldioides*. (a) One-half of a *Supaia* leaf (leaves were forked) illustrating typical morphology and preservation as a mold. USNM specimen 618980, USGS locality 8977. (b) Close-up of three lower left pinnules in image (a), showing strong pinnule midvein and arching, but vaguely fasciculate, open dichotomous, lateral venation. (c) Fragmentary specimen illustrating typical frond shape. USNM specimen 618981, USGS locality 8977. (d) Fragmentary specimen clearly showing the vaulted character of the pinnules, the ends of which have been broken; pinnule bases appear to be constricted because of their irregular thickness and vaulting, resulting in partial burial of the decurrent leaf bases. USNM specimen 618979, USGS locality 8952. Scale bars = 1 cm.

FOSSIL FLORA

The base of the Red Magdalena flora is small, consisting of 81 fossiliferous quadrats and 46 blank surfaces. The high frequency of nonfossiliferous surfaces indicates relative sparseness of the plant material and its confinement to one or a few layers.

Walchian conifers are the most abundant plants in the assemblage. These include the following morphotypes.

Morphotype A (22.2% frequency of occurrence; see Methods of Analysis section) is represented by isolated shoots and several plagiotropic penultimate branch systems with ultimate shoots attached (e.g., Figure 6b,c). The ultimate leaves are falcate in profile, with keels on both sides of the leaf; they bifacially flatten distally (cf. Type I leaves; de Laubenfels, 1953). The leaves are narrow triangular to linear with obtuse apices in face view. The leaf attachment areas are rhomboidal in shape. Leaves are 3–4 mm in length. Leaf widths range from 0.5 to 1.0 mm midleaf and are slightly wider at the base. Leaf thickness is 1 mm or less at the base and thins out distally. The leaves depart at high angles, 80°–130°; these angles are quite variable but consistent within specimens. One branch specimen in which the leaf attachment is obscured may be an ovuliferous cone (Figure 6d).

Morphotype B (60.5%) is represented by isolated shoots and several plagiotropic penultimate branch systems with ultimate shoots attached (Figure 7a–d). Penultimate leaves are up to 5 mm in length. Ultimate leaves are helically arranged, slightly curved in profile, and in some wider specimens distally bifacially flattened and have an incurved apex (cf. Type III leaves; de Laubenfels, 1953). The leaves are narrow triangular to linear with obtuse apices in face view. Ultimate leaf lengths range from 2 to 4 mm, with widths of 0.4–1.2 mm and a thickness of 0.3–0.5 mm or less. The leaves depart at low angles, 20°–50°, which is generally consistent within specimens.

Morphotype C is represented by two plagiotropic antepenultimate branch systems, with penultimate branches departing the antepenultimate branch at angles of 20°–60°, with lower angles near the branch apex (mean values for the individual specimens are 45° and 38°) and ultimate branches leaving at angles of 30°–60° (means for individual specimens are 43° and 51°). One of these branch systems is not fully developed and shows sprays of foliage in its penultimate and ultimate shoots (Figure 6a); in order to differentiate the dimensions of these immature leaves from the mature forms, their dimensions are shown within brackets below. The other branch system is fully developed. The antepenultimate leaves are slightly curved, bifacially flattened, narrowly triangular in face view, 4.0–4.5 mm in length, 0.7–1.0 mm in width, and arise at an angle of 50°–60°. The penultimate leaves are slightly curved to falcate, bifacially flattened, narrow triangular in face view, 2.8–3.5 [1.3–2.4] mm long, and 0.6–0.7 [0.4–0.6] mm wide. They depart at a mean angle of 45° in the partially immature specimen and at about 60° in the other; these angles are larger when an ultimate shoot arises from the leaf axil.

Ultimate leaves are helically arranged and slightly curved in profile, with a slightly incurved apex (cf. Type III leaves; de Laubenfels, 1953). The leaves are linear with obtuse apices in face view. Leaf lengths range from 1.5 to 2.4 [1.0 to 1.5] mm, and leaf widths are 0.5–0.6 [0.3–0.6] mm. Leaves are 0.3–0.5 mm or less in thickness. The leaves depart at low angles, 30°–55° [45°–70°], and are generally consistent within a single specimen. Leaf morphology of this type is comparable to that of Morphotype B; the two shoot specimens might represent different orders of branch systems and/or might be from different positions on the tree.

Morphotype D (3.7%) is represented by isolated shoots (Figure 5a). The helically arranged ultimate leaves are straight in profile, with an inwardly curved apex and a keel on the adaxial side of the leaf. Leaf shape in face view and leaf width are not known. Leaf length is 3–7 mm, and leaf thickness is ~0.7 mm, thinning out distally. The leaves depart at angles between 45° and 80°.

A single polliniferous cone (Figure 7e) was found that is probably associated with one of these conifer morphotypes.

The remainder of this flora consists of plants that all occur at low frequencies.

CALAMITALEANS. Calamitaleans are the only certain pteridophytes in the flora. The remains consist of fragments of foliage attributable to *Annularia* sp. (3.7%) and a single possible calamitalean stem (1.2%), lacking a node but with regular ribbing too coarse to represent the veins of cordaitalean foliage and too regular to be sclerenchymatous bundles of a tree fern or pteridosperm axis (Figure 6e, right side).

TAENIOPTERIS SP. CF. *T. ABNORMIS* (2.5%). Two small fragments of *Taeniopteris* sp. cf. *T. abnormis* foliage were found in the collection. The illustrated specimen (Figure 6e, left side) appears to come from near the apex of a leaf, given the up-curved aspect of its veins, which are rarely branched. The intact apex was likely broad and rounded. The other specimen shows a relatively wide midvein and perpendicular, sparsely branched lateral veins. The taxonomy of *Taeniopteris* is complicated because so many species have been named from isolated specimens. Not common in European Late Pennsylvanian and Permian floras, *Taeniopteris* is quite common in American floras, particularly of early Permian age; see discussion in Barthel (2009) or Wagner and Martínez García (1982).

CORDAITES SP. (1.2%). A single, questionable fragment of a possible cordaitalean leaf was identified (Figure 8a). This specimen may, in fact, be a striate axis, assignable to the pteridosperms, possibly *Odontopteris* (*Mixoneura*) sp. cf. *O. schlotheimii*. It is not certain that the longitudinal striations are straight and unbranched enough to be leaf veins, although they appear to be so. In addition, the very flat aspect of the specimen suggests a leaf rather than a flattened axis. The specimen is encrusted with spirorbids, which suggests a period of flotation prior to burial, again consistent with a flat, individual leaf blade rather than a stem.

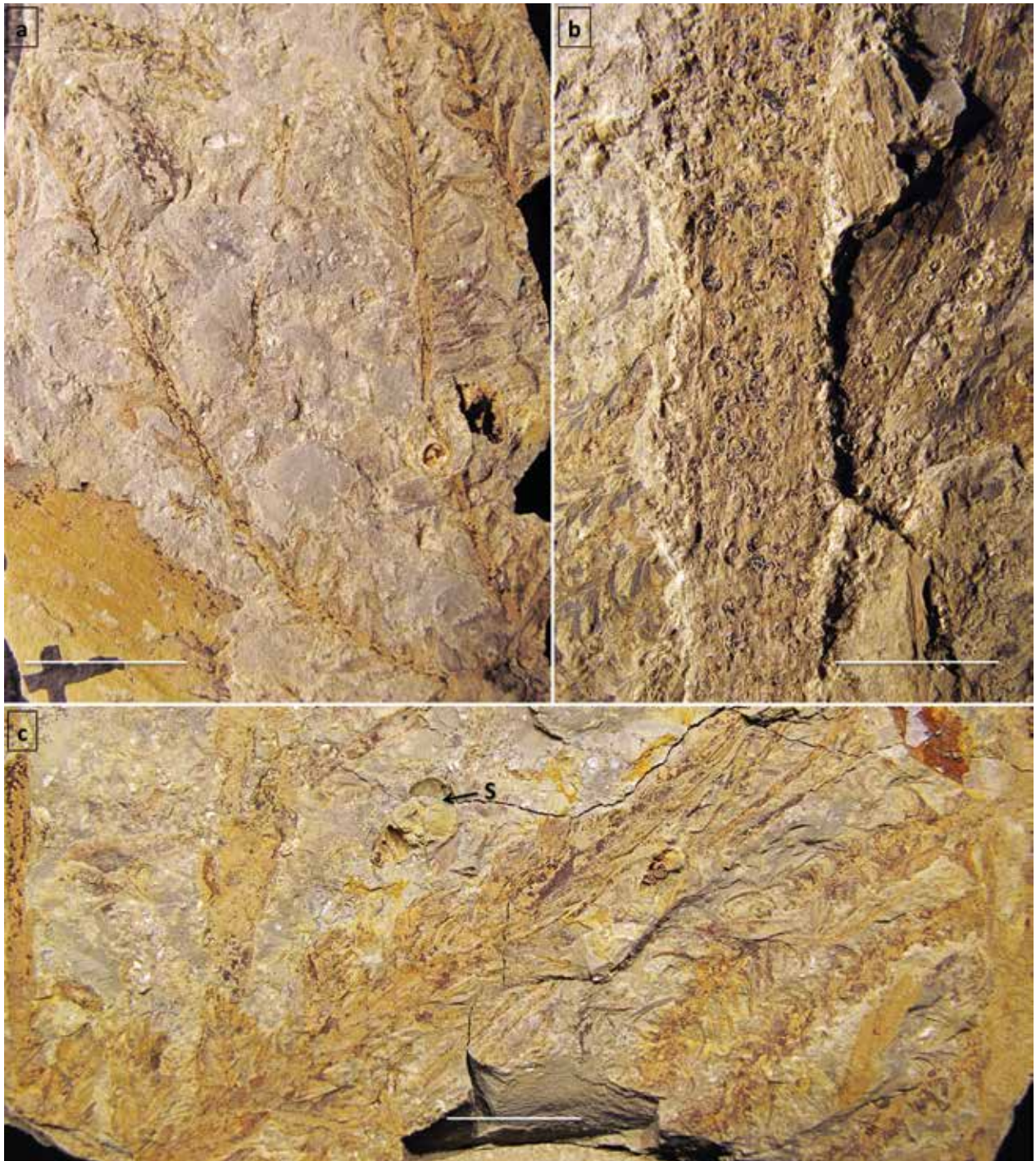


FIGURE 5. Base of the Red Magdalena, animal fossils. USGS locality 8951. (a) Ostracods (small, white, bean shaped) in sediment surrounding walchian conifer Morphotype D. USNM specimen 618982. (b) Microconchids/spirorbids attached to taxonomically indeterminate axes and to foliage of a walchian conifer. USNM specimen 618983. (c) Mold of a snail (at S, arrow) and ostracods in sediment surrounding a branch of walchian conifer Morphotype B. USNM specimen 618984. Scale bars = 1 cm.



FIGURE 6. Base of the Red Magdalena, USGS locality 8951. (a) Walchian conifer Morphotype C antepenultimate branch fragment; the penultimate and ultimate shoots are still developing. USNM specimen 618990. (b) Walchian conifer Morphotype A branch fragment with larger leaves, also showing the oblique insertion of leaves. USNM specimen 618991. (c) Walchian conifer Morphotype A of “typical” morphology. USNM specimen 618992. (d) Walchian conifer Morphotype A possible ovuliferous cone shown in a section with the external cover of leaves/bracts removed. USNM specimen 619252. (e) *Taeniopteris* sp. cf. *T. abnormis* (left side) and possible calamitalean stem (right side). USNM specimen 618993. Scale bars = 1 cm.



FIGURE 7. Base of the Red Magdalena, USGS locality 8951, walchian conifers, comparative morphology. (a) Walchian conifer Morphotype B branch fragment. USNM specimen 618985. (b) Walchian conifer Morphotype B branch fragment. USNM specimen 618986. (c) Walchian conifer Morphotype B branch fragment. USNM specimen 618987. (d) Walchian conifer cf. Morphotype B branch fragment. Note that leaves are smaller and more closely adpressed to the axes than in the other illustrated specimens. USNM specimen 618988. (e) Walchian polliniferous cone or bud. USNM specimen 618989. Scale bars = 1 cm.

ODONTOPTERIS (MIXONEURA) SP. CF. O. SCHLOTHEIMII (10%). Various pinnule fragments were found that have relatively sparse venation that departs steeply from the midvein area (a midvein is not well developed but may consist of a concentration of veins), arches through the lamina, and meets the margin at nearly a right angle (Figure 8b–e). Where lateral pinnules are clearly developed (Figure 8d), multiple veins enter the lamina, and a midvein is absent to only weakly developed. Overall, the pinnules we assign to this species are quite variable. However, the combination of specimens with an undulatory margin (Figure 8b), elongate triangular shape (Figure 8c,e), or triangular shape with a bluntly attenuated apex where small individual pinnules are developed (Figure 8d) is broadly consistent with *Odontopteris (Mixoneura) schlotheimii* (e.g., Barthel and Amelang, 2011). Note that *Mixoneura* has been considered by some authors to be a distinct genus (see Wagner and Castro, 1998); because of its complex nomenclatural history, we use it here parenthetically and as a subgroup of *Odontopteris*.

RHACHIPHYLLUM SP. CF. R. SCHENKII (4.9%). *Rhachiphyllum* is a callipterid, a group of peltaspermous seed plants segregated from the genus *Callipteris* (Kerp and Haubold, 1988). Specimens assigned to this species are superficially quite like some of those attributed to *Odontopteris (Mixoneura) schlotheimii* in having sparse secondary venation and a somewhat odontopteroid aspect due to the entry of secondary veins into the lamina directly from the supporting rachis (Figure 8f). However, these lateral veins ascend steeply and meet the margin at an acute angle. They also have a well-developed, albeit thin, midvein that is not sunken into the lamina surface (as in *Autunia*). The tearing of the lamina in some of the specimens (as seen in the left-hand specimen in Figure 8f) also indicates a thin pinnule lamina. In keeping with this assignment, a small, fragmentary specimen with similarities to *Peltaspermum* sp., the reproductive organ of various types of callipterids, a subgroup of the peltasperms (Kerp and Haubold, 1988; Poort and Kerp, 1990), was identified in the collection (Figure 8g).

The remainder of the plant material consists of fragmentary pinnules of a neuropteroid aspect that are not specifically determinable (3.7%); rare seeds ($n = 2$, 2.5%); striate axes, possibly of pteridosperms (7.4%); and woody axes, probably from conifers ($n = 2$, 2.5%).

AGE AND ENVIRONMENTAL IMPLICATIONS OF THE FLORA

If, as we suggest, the Red Magdalena correlates approximately with the Bursum Formation, then there is a published flora by Tidwell et al. (1999; with additional illustrations in Ash and Tidwell, 1982) with which it can be compared, from the Red Tanks Member of the Bursum Formation at Carrizo Arroyo in the Lucero uplift of Valencia County. The Red Tanks Member is equivalent to the dominantly nonmarine facies of the Bursum Formation as the term is used elsewhere in the state, placing it at

the Pennsylvanian–Permian boundary. The important similarities between the large Carrizo Arroyo assemblage and the small collection made in Abo Pass are the following: (1) conifer dominance of a largely seed-plant flora, (2) conifer morphotypes that are the same as those identified by Tidwell et al. as *Walchia piniiformis*, *Walchia schneideri*, and *Ernestiodendron filiciforme*, (3) common mixoneurid odontopterids, including forms attributed to *Neuropteris pseudoblissii*, which may, in fact, be *Odontopteris (Mixoneura) schlotheimii*, and also some similar in form to those reported here with elongate, triangular pinnules/pinnulae, (4) common callipterids, including *Rhachiphyllum schenkii*, and (5) few pteridophytes, but including calamitaleans, which are nearly ubiquitous in late Paleozoic floras, even from strongly seasonally dry settings, seemingly occupying even ephemeral wet areas. The more intensively sampled Carrizo Arroyo flora also includes a slightly wider array of medullosan pteridosperms, more abundant cordaitaleans, and common *Sphenopteris germanica* (previously identified as either *Sphenopteridium manzanitanum* or *Arnophyton kuesii*), plus such species as *Charliea manzanitanum* and *Phasmatocycas*.

The authors also have collected extensively in the Bursum Formation, both in central and southern New Mexico, and have found a flora similar to that reported by Ash and Tidwell (1982) and Tidwell et al. (1999). A brief mention and illustration of the dominant plants in these floras from Socorro County to the southwest of Abo Pass are in Lucas et al. (2013). Key findings from these studies are that the Bursum floras are dominated primarily by conifers, with locally common to abundant cordaitaleans, *Taeniopteris*, *Sphenopteris germanica*, and callipterids, the latter most commonly represented by *Rhachiphyllum schenkii*. However, there is considerable site-to-site variation in composition, including local abundance of marattialean tree fern foliage (*Pecopteris*).

From a biostratigraphic point of view, there are virtually no taxa of the Abo Pass Red Magdalena flora or of presumably similar aged floras in Carrizo Arroyo or Socorro County that will permit an unequivocal age assignment, apart from being near the Pennsylvanian–Permian transition. The floras bear a resemblance to those of the Rotliegend, as characterized in detail by Barthel (2009).

The abundant occurrence of freshwater to brackish-water invertebrates indicates these assemblages occupied a coastal or estuarine setting. Tidwell et al. (1999) discuss the possible setting of the Carrizo Arroyo Bursum flora and address the conflict that exists between interpretations that place the flora in the “uplands” and those that attribute its composition to a climate of seasonal drought. Here, we stand firmly on the side of a climatic interpretation—the plants were most likely growing close to the environment in which they were deposited, and that environment was in the lowlands. The near absence of pteridophytes (spore-producing ferns, lycopsids, sphenopsids) in the flora and strong dominance of xeromorphic seed plants suggest conditions of periodic moisture stress, perhaps a dry subhumid climate in the terminology of Cecil (2003).

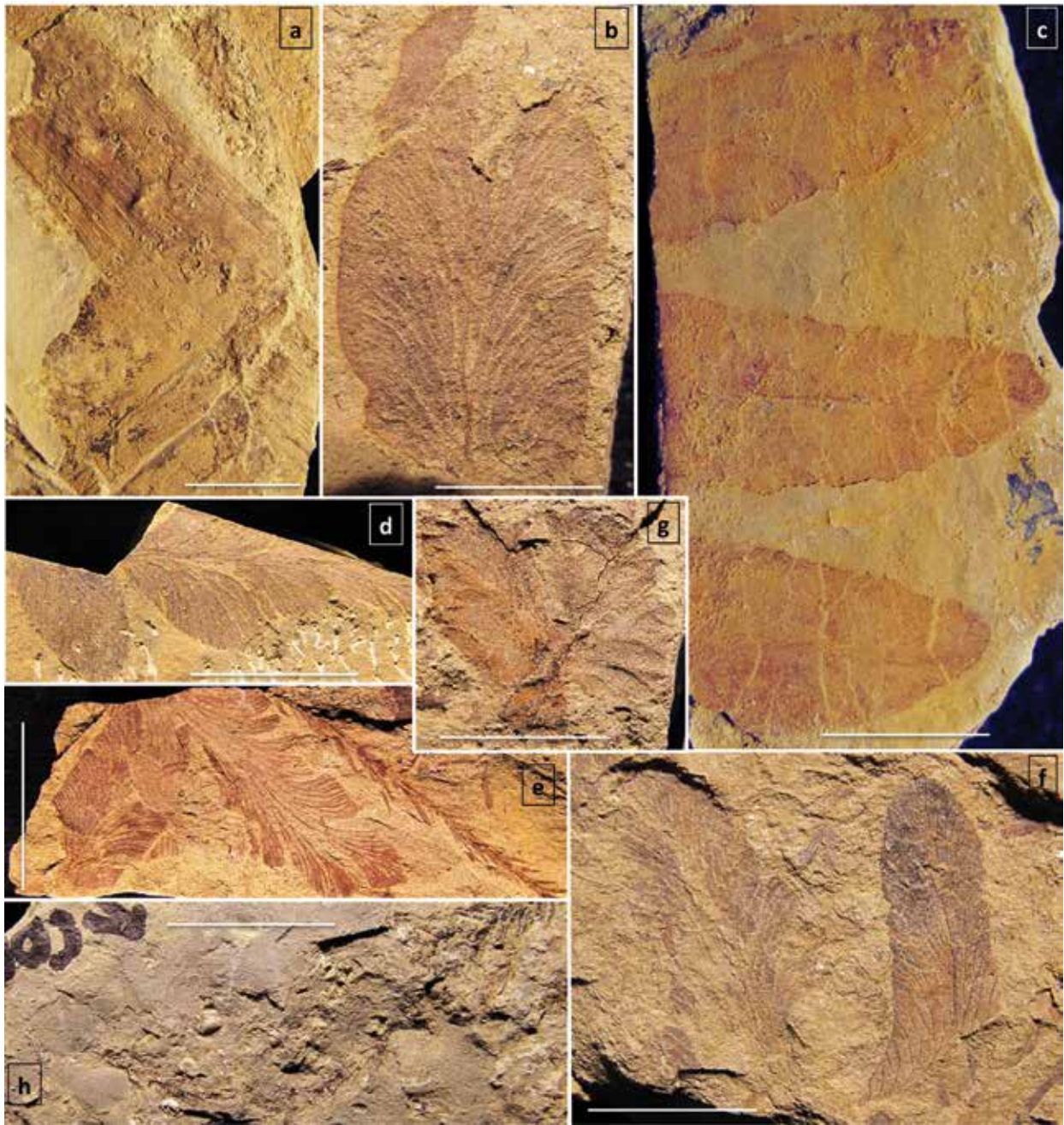


FIGURE 8. Base of the Red Magdalena, USGS locality 8951. (a) Cordaitalean leaf fragment. Note flat aspect and fine longitudinal striations (veins). Microconchids are attached to the surface. USNM specimen 618994. (b) *Odontopteris* (*Mixoneura*) *schlotheimii* pinna terminus; note undulatory margins. USNM specimen 618995. (c) *Odontopteris* (*Mixoneura*) *schlotheimii*; several terminal portions of pinnae likely originally attached to a common rachis. USNM specimen 618996. (d) *Odontopteris* (*Mixoneura*) *schlotheimii*, pinnate portion of a pinna. Pinnules have rather widely spaced veins. USNM specimen 618997. (e) *Odontopteris* (*Mixoneura*) *schlotheimii*, pinna segments. Note strong arc of veins as they approach the margins. USNM specimen 618998. (f) Compare with *Rhachiphyllum schenkii*. Pair of pinnules with thin, but clearly marked midvein and steeply ascending, relatively straight lateral veins that meet the margin without changing trajectory. USNM Specimen 618999. (g) Compare with *Peltaspermum* type, radially symmetrical, reproductive organ, fragmentary preservation. USNM specimen 619001. (h) Ostracods in sediment surrounding walchian conifer branch. USNM specimen 619000. Scale bars = 1 cm.

UNIT 8

Read's Unit 8 collection, USGS locality 8974, consists of fossil plants on pieces of light to medium gray, slightly silty claystone that is blocky in character and may be very finely laminated, although this is difficult to see in hand samples. Bedding surfaces are broad and flat, and the plant remains give no indication of crossing these horizontal surfaces. Plant fossils are preserved as organic compressions with some staining by iron minerals. There commonly are halos of reduced iron around plant remains. The plant fossils are mainly fragmentary and of relatively small size. They appear to have been transported into the depositional environment, which, from the character of the rock matrix, was a site of quiet-water sedimentation, perhaps a lake. However, no CPD was noted among the plant fossil remains or draping bedding surfaces. Comminuted plant debris might be expected in a low-energy depositional setting into which streams were debouching, carrying various sizes of plant litter; perhaps the size of the catchment was large, accounting for both the small size of the plant fragments and the absence of CPD, which may have been diluted by dispersal. No fossil charcoal was identified in the collection.

Included among the plants were several kinds of animal fossils. These include a single fragment of an insect wing. Among the aquatic organisms are conchostracans, ostracods, and a single linguloid, inarticulate brachiopod. Common to abundant ostracods and a single linguloid suggest brackish-water conditions, although the linguloid may have been transported given the principally marine preferences of these organisms (Emig, 1986). The conchostracans, which are abundant in the collection, are indicative of ephemeral standing-water conditions, mainly fresh but occasionally brackish (Frank, 1988; Brendonck, 1996); they may reflect fluctuation in the areal extent of the depositional environment, with marginal drying, or possibly seasonal rainfall variation, resulting in ephemeral periods of standing water on the land surface surrounding the depositional setting.

FOSSIL FLORA

The collection consists of 140 total hand-sample surfaces; 95 surfaces contained some form of identifiable plant remains, and 45 were barren.

The dominant element of the fossil flora is the fern or seed fern *Sphenopteris germanica* (26.3%; Figure 9a,b). This plant has been characterized as *Sphenopteridium manzanitanum* in floras and floral lists from the western United States, following its description under that name by Mamay (1992; see discussion of the taxonomy of this plant in DiMichele et al., 2013b). The *Sphenopteris germanica* in this collection is variable in form, and on many specimens, the pinnule lobes are rounded and held at somewhat lower angles than seen in specimens of Missourian age from the Kinney Brick Quarry locality in the Manzanita Mountains (*Sphenopteridium manzanitanum*). Some of the specimens we have identified as *S. germanica* are labeled "*Callipteris lyratifolia*" or "*Odontopteris obtusa*" in the collection (presumably by Charles B. Read).

Two or three types of conifer occur in the flora (13%), all at low to moderate abundances. Most specimens conform to Morphotype B (Figure 9f) and have curved, but not adpressed, bilaterally flattened leaves. Others, however, have leaves that are significantly more gracile, elongate, and positioned to suggest differentiation from Morphotype B and may be Morphotype A (Figure 9e). Some specimens have shorter leaves disposed in a manner similar to those of Morphotype B. Without cuticular anatomy it is difficult to identify strictly vegetative material.

The flora appears to contain two distinct forms of mixoneurid odontopterids, *Odontopteris* (*Mixoneura*) *schlotheimii* and *Odontopteris* (*Mixoneura*) *subcrenulata*, which were not recognized as distinct during the quantification. Together, they occur at a frequency of 16.8%. Because some of the pinnules of these plants are of distinctly triangular shape and have neuropterid features, we originally identified many of them as *Neuroodontopteris auriculata*.

The main portion of the material in question is attributable to *Odontopteris* (*Mixoneura*) *schlotheimii*, which is characterized by large, somewhat irregularly to triangularly shaped pinnules with relatively sparse, fine, open dichotomous venation (Barthel and Amelang, 2011). The larger specimens in the Unit 8 collection have relatively widely spaced lateral veins, undulatory pinnule margins, and triangular pinnule shape (Figures 9g,h, 10n). Some pinnules show differentiation into small, round, basal pinnule lobes or even free pinnules at the base, but these also have sparse, fine veins. In rare instances, pinnules were encountered (Figure 10n), always of larger size classes, in which vein anastomoses were identified, particularly near the pinnule apex but occasionally in the lobed basal portions. Because venation in these pinnules and their overall shape are similar to those of *O. schlotheimii*, we presume a common identity with that species, although such vein reticulations may indicate that erection of a new species is called for.

A few of the mixoneuroid specimens appear to be most similar to *Odontopteris* (*Mixoneura*) *subcrenulata* (Figure 10b–d). All have dense, fine venation, which enters a pinnule base centrally. The illustrated specimens show a rank of small, nearly round, broadly attached pinnules (Figure 10b), an elongate pinnule with a slightly undulatory margin (Figure 10c), and a series of pinnules possibly representing a transition from free, small pinnules to an entire, larger terminal pinnule (Figure 10d). These remains are also similar to *Odontopteris* (*Mixoneura*) *lingulata*. The two species can be difficult to distinguish on the basis of small fragmentary specimens. In Europe, *Odontopteris* (*Mixoneura*) *subcrenulata* is a predominantly Stephanian species, whereas *O. lingulata* is a typical Rotliegend species. *Odontopteris lingulata* differs from *O. subcrenulata* in having very long, tongue-shaped terminal pinnules, which may be up to half the pinna length. Hence, the number of normal pinnules per pinna is relatively low, and they are rather widely spaced. *Odontopteris subcrenulata* has much shorter terminal pinnules, and normal pinnules stand more closely together. The venation also is different: in *O. subcrenulata* a bundle of veins enters the pinnule approximately in the middle of the pinnule base, whereas in

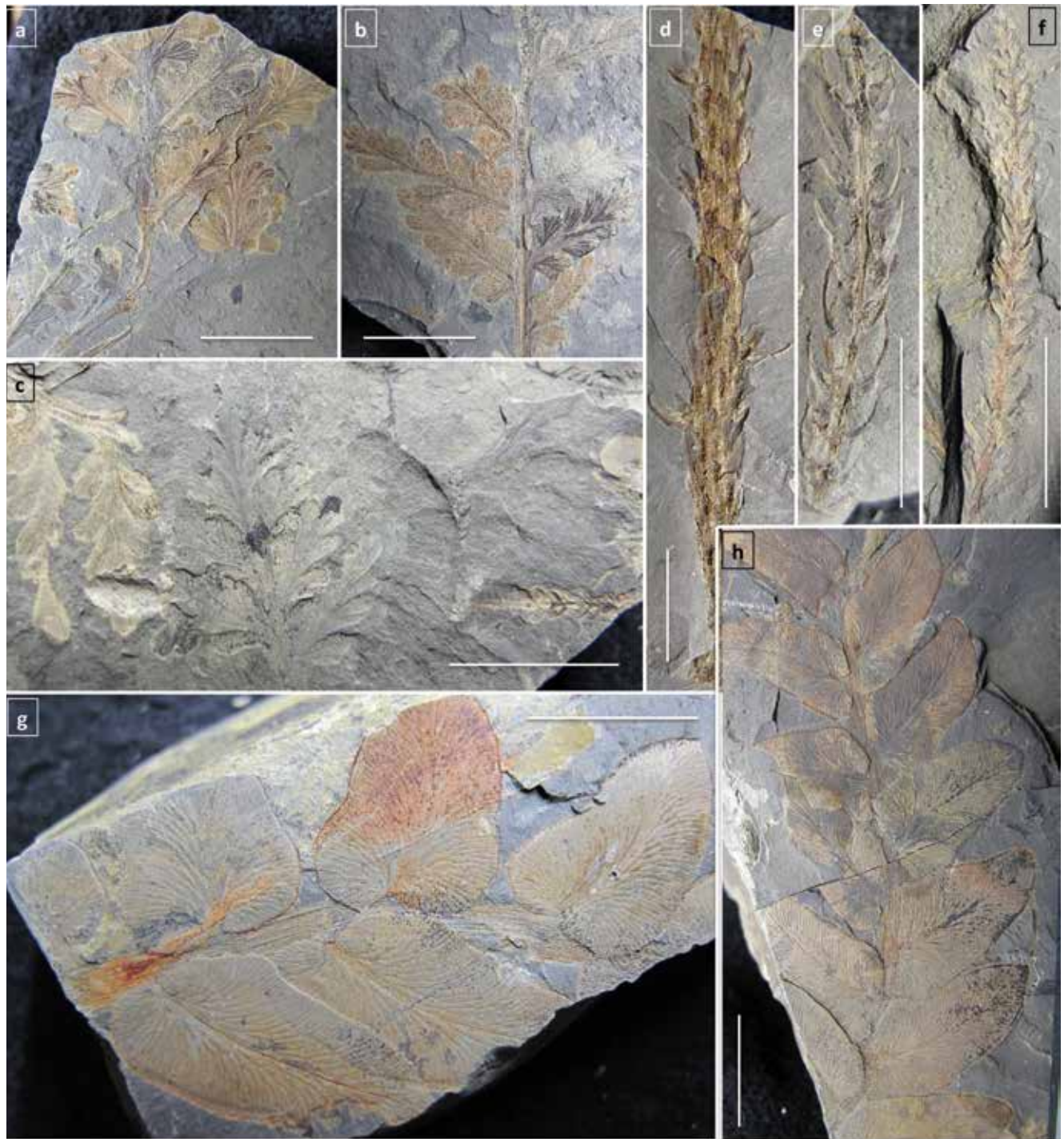


FIGURE 9. Unit 8, USGS locality 8974, dominant elements. (a) *Sphenopteris germanica*. USNM specimen 619003. (b) *Sphenopteris germanica*. USNM specimen 619002. (c) *Sphenopteris germanica* and a walchian conifer fragment. USNM specimen 619004. (d) Walchian conifer fragment of lateral branch main axis. USNM specimen 619005. (e) Walchian conifer. USNM specimen 619007. (f) Walchian conifer Morphotype B. USNM specimen 619006. (g) *Odontopteris (Mixoneura) schlotheimii*. USNM specimen 619008. (h) *Odontopteris (Mixoneura) schlotheimii*. USNM specimen 619009. Scale bars = 1 cm.

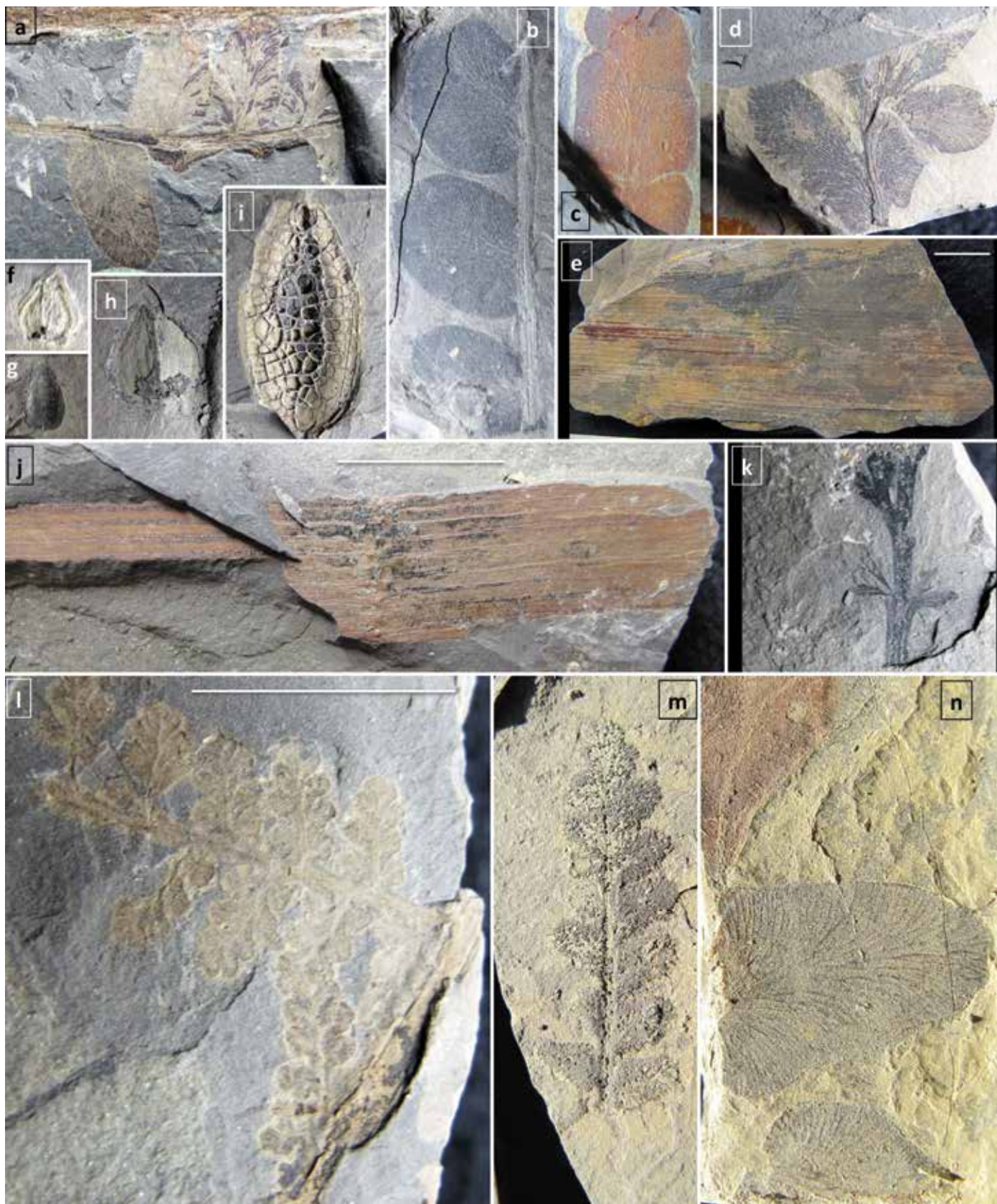


FIGURE 10. (Facing page) Unit 8, USGS locality 8974, minor elements. Scale bar in image (j) applies to all images without scale bars. (a) Neuropteroid pinnules, possibly assignable to *Neurodopteris auriculata* but also possibly *Odopteris (Mixoneura) schlotheimi*. USNM specimen 619010. (b) *Odopteris (Mixoneura) subcrenulata*, free, rounded pinnules at base of pinna. USNM specimen 619011. (c) *Odopteris (Mixoneura) subcrenulata*, transition from free pinnules to broad, neuropteroid lamina. USNM specimen 619012. (d) *Odopteris (Mixoneura) subcrenulata*, free pinnules transitioning to broad, neuropteroid lamina, perhaps near pinna apex. USNM specimen 619013. (e) Cordaitalean leaf. USNM specimen 619014. (f)–(i) Various shapes and sizes of seeds found in the collection, all singletons and not clearly associated with any particular type of vegetative foliage. USNM specimens (f) 619015, (g) 619016, (h) 619017, and (i) 619018. (j) Calamitalean stem. USNM specimen 619019. (k) Possibly a *Sphenophyllum* specimen, but of uncertain specific affinity. USNM specimen 619020. (l) *Sphenopteris* sp., possibly groundcover fern foliage. USNM specimen 619021. (m) *Sphenopteris* sp., also possibly foliage of a groundcover fern. USNM specimen 619023. (n) Pinnules with general characteristics of *Odopteris (Mixoneura) schlotheimii* but with reticulations of the lateral veins in the apical portion of the pinnule. USNM specimen 619022. Scale bars = 1 cm.

O. lingulata veins enter the pinnule over the entire pinnule width and are not bundled. These two species are considered synonymous by some authors (see Wagner and Castro, 1998, for discussion).

The only other seed plant in the flora is represented by foliage of *Cordaites* (6.3%). All such leaves are fragmentary but of low aspect, elongate, and with fine, relatively dense, parallel venation (Figure 10e).

There are few pteridophytic taxa among the plant remains. Those identified include calamitalean stems (8%; Figure 10j) and foliage, *Annularia* sp. cf. *A. spicata*. Groundcover is suggested by two specimens tentatively assigned to *Sphenophyllum* sp. (Figure 10k) and single fragments of two different kinds of sphenopterid fern (Figure 10l,m). With regard to the matter of groundcover, *Sphenopteris germanica* also may have been a small, centrally rooted plant with a cormose stem (DiMichele, Kerp, Lucas, and Chaney, unpublished data), a small, juvenile specimen that Ash and Tidwell (1987) described as *Arnophyton kuesii*. Seeds of several kinds, all relatively small, occur on 9% of the quadrats (Figure 10f–i). Unidentifiable woody or striated axes were identified on 25% and 16% of the quadrats, respectively.

STRATIGRAPHIC AND ENVIRONMENTAL INTERPRETATIONS

The Unit 8 flora is most likely from the upper portion of Read's Abo Pass section. The floral elements, particularly *Odopteris (Mixoneura) schlotheimi* and *O. subcrenulata*, are typical of Late Pennsylvanian floras. The presence of conifer remains also is typical of western Pangean floras of this time interval; conifers have been identified in strata as old as Middle Pennsylvanian in New Mexico (Lucas et al., 2013). *Sphenopteris germanica* had been considered diagnostic of Permian-aged strata (e.g., Pfefferkorn and Resnick, 1980) but also has been identified, often in considerable abundance, in strata as old as Middle Pennsylvanian (Lucas et al., 2013; see also DiMichele et al., 2013b, for discussion of the taxonomic issues surrounding the differentiation of *Sphenopteris germanica* and *Sphenopteridium manzanitanum*).

The presence of *Sphenopteris germanica*, walcchian conifers, and species of mixoneurid-type *Odopteris* and the absence of pecopterid ferns and neuropterid pteridosperms suggest a seasonally dry climatic setting, perhaps dry subhumid (Cecil, 2003). This is consistent with the presence of conchostracans among the faunal remains. Such seasonally dry environmental conditions also are reflected in the generally common occurrence of floral elements such as conifers, callipterids, and exotic elements, such as *Charliea*, *Plagiozamites*, or even *Podozamites*, in western Pangean floras earlier than their common occurrence in floras of coal basins in central Pangea (the U.S. Midcontinent through Europe). For example, compare the stratigraphic ranges of many of these plants as reported in Kerp and Fichter (1985), Blake et al. (2002), Barthel (2009), and Wagner and Álvarez-Vázquez (2010). These plants appear to have been common throughout much of western Pangea from at least the Middle Pennsylvanian onward and perhaps earlier. Their occasional appearances in coal basins of central Pangea as early as Middle Pennsylvanian (e.g., Falcon-Lang et al., 2009) most likely reflects the increased intensity of periods of seasonal aridity at this time during certain portions of glacial-interglacial cycles (Rosenau et al., 2013), which were closely synchronized with changes in both sea level and tropical climate (Cecil et al., 2003, 2014).

UNIT 10

Unit 10, USGS locality 8975, is the largest collection of the Abo Canyon section. The plant fossils are encased in a brown-tan siltstone. The siltstone does not have notable sedimentary structures, such as ripples or other bed forms. Rather, the matrix appears to be massive, and specimens often split irregularly across bedding surfaces. The plant fossil remains frequently are confined to one surface of the specimen, the reverse sides of nearly a third being barren, suggesting pulsed transport and intermittent deposition of plant material. This type of deposition is further suggested by abundant CPD in the Unit 10 collection (Figure 11a), including up to 3.5-cm-thick plant-hash

conglomerate layers within a siltstone matrix that includes small flakes of muscovite, various-sized silt grains, and small, rounded quartz granules.

Within the CPD layers the silt matrix splits irregularly, although the plants mostly appear to be horizontally disposed, suggesting a slurry, but one within which the organic matter could settle somewhat gently. Whereas muscovite is common in the siltstone, it occurs more abundantly in association with the CPD deposits, especially in layers just above or below the CPD layers. Many identifiable plants are found among the CPD. Despite the abundance of plant debris and small organic clasts, only a single, questionable specimen of charcoal was identified in the collection.

Small animal remains are found both within the CPD layers and preserved within the siltstones. These include spirorbids/microconchids (Figures 11b, 13b) and small snails (Figures 11b, 13b). The spirorbids occur only in attachment to plant remains, including calamitalean stems, cordaitalean foliage, neuropterid foliage, and, most rarely, conifer branches. Such remains suggest a brackish-water to freshwater environment of deposition (Taylor and Vinn, 2006; we do not accept the argument of Gierlowski-Kordesch and Cassle [2015] for restriction of microconchids to exclusively marine salinities).

FOSSIL FLORA

A total of 384 quadrats were examined; 269 were fossiliferous and were used in the quantitative analysis, whereas the remaining 115 were barren. The flora is dominated by conifers, which occur on over 60% of the fossiliferous quadrats.

Walchian conifers account for the bulk of this material, occurring on 56.5% of all fossiliferous quadrats. Most of these conform broadly to Morphotype B (Figure 12a,b,d,e); a small number of specimens (1% of all quadrats) have relatively triangularly shaped leaves that are more adpressed against the stem than in most of the specimens (Figure 12f). A small number of specimens (2.6% of all quadrats) fall into Morphotype D in having leaves that are much longer than those of other walchians and positioned at a low angle, just above orthogonal with the stem (Figure 12c); the leaves are very straight through most of their length, making a narrow angle with the stem at their base before bending to a lower-angle position and again turning upward abruptly at their tips. Morphotype A (Figure 13a,b) occurs at a frequency of approximately 12% of the quadrats. Nearly all the remains are of vegetative foliage with its distinctive morphology, the leaves inserted at right angles or even obliquely prior to turning up sharply in their outer $\frac{1}{2}$ to $\frac{2}{3}$. A single specimen was found with several compound ovuliferous cones (Figure 13c).

A single stem was found with distinctive leaf scars and attached walchian-type leaves (Figure 14a). In addition, several parts of walchian reproductive organs also were found, including a possible cone axis with subtending bracts/leaves (Figure 13d), buds or small polliniferous cones (Figure 14b), and bracts from ovuliferous cones, including *Gomphostrobus* (Figure 14c) and bracts of uncertain affinity (Figure 14d).

Minor elements of this flora include the following presumptive seed plants: Mixoneurid *Odontopteris* (5.9%) is represented by two species, *Odontopteris* (*Mixoneura*) *schlotheimii* (Figure 15a–d) and *Odontopteris* (*Mixoneura*) *subcrenulata* (Figures 15e–g, 16a). These may be differentiated by the lower vein density and thus sparser venation of *O. schlotheimii*, its somewhat more neuropteroid terminal pinnules or pinnae, and the more rectangular nature of small, individual pinnules. The smaller pinnules of *O. subcrenulata*, by contrast, are more rounded.

A single specimen is possibly attributable to the callipterid *Rhachiphyllum* sp. (Figure 15h,i). This single complete pinnule and a fragment of another, likely from the same rachis, have an elongate shape with a decurrent base, parallel sides, and a rounded apex. The midvein is thin and not sunken; that is to say, the laminae of the pinnules are not vaulted. Lateral veins are relatively sparse but are steeply ascending and do not show inflections toward the margin as they approach, but rather maintain their straight, steep path. A single specimen of the callipterid reproductive structure, *Peltaspermum*, was identified; however, the partial preservation of this specimen leaves open affinity with *Remia* (Figure 17l). There is a single occurrence of small valvate organs that may be peltasperm pollen organs (Figure 14n).

Relatively large, reticulate-veined pinnules with meshes resembling those of *Reticulopteris muensteri* (5.6%; Figure 16b,c) are among the most unusual specimens in this assemblage. *Reticulopteris muensteri* is typically found in strata of Westphalian/Moscovian age. In consideration of the rest of this flora, therefore, this seems an unlikely identification. Late Pennsylvanian reticulate-veined neuropteroid plants that may be considered possible candidates for identity include *Barthelopteris germarii* and *Linopteris neuropteroides*. However, the vein meshes in the Unit 10 pinnules are concentrated near the midvein, are very large and open, and do not parallel the midvein. The lateral veins turn sharply toward the margin of the pinnule and, through an elongate, flattened trajectory, meet it at right angles. The number of vein anastomoses in the middle and outer areas of the lamina is small compared to those near the midrib. This pattern is much more like that of *Reticulopteris* than either *Barthelopteris germarii* or *Linopteris neuropteroides*, where the vein meshes are smaller, more uniformly distributed across the pinnule lamina, and more parallel with the midvein; in addition, the lateral vein path to the margin is more arcuate in these latter species (see Zodrow and Cleal, 1993; Zodrow et al., 2007). The Abo Pass Unit 10 specimens may indicate the existence of a new species of *Reticulopteris*. However, given the age uncertainties of the flora in the absence of Charles B. Read's field notes and given that this potentially new species would be known from only a handful of isolated pinnules, we feel it best to defer such a description until, and if, more supporting information or additional, more complete specimens become available. Isolated pinnules of similar shape and venation have been found at a few other locations in New Mexico but provide no additional information on possible affinities or gross frond morphology (see further



FIGURE 11. Unit 10, USGS locality 8975, comminuted plant debris and animal fossils. (a) Comminuted plant debris covering a bedding surface. USNM specimen 619051. (b) Microconchids/spirorbids attached to pinnules of *Odontopteris* (*Mixoneura*) *schlotheimii*. USNM specimen 619024. (c) Small snail in sediment surrounding walcian conifer branches and microconchids/spirorbids attached to calamitalean stem fragments on right. USNM specimen 619052. Scale bars = 1 cm.

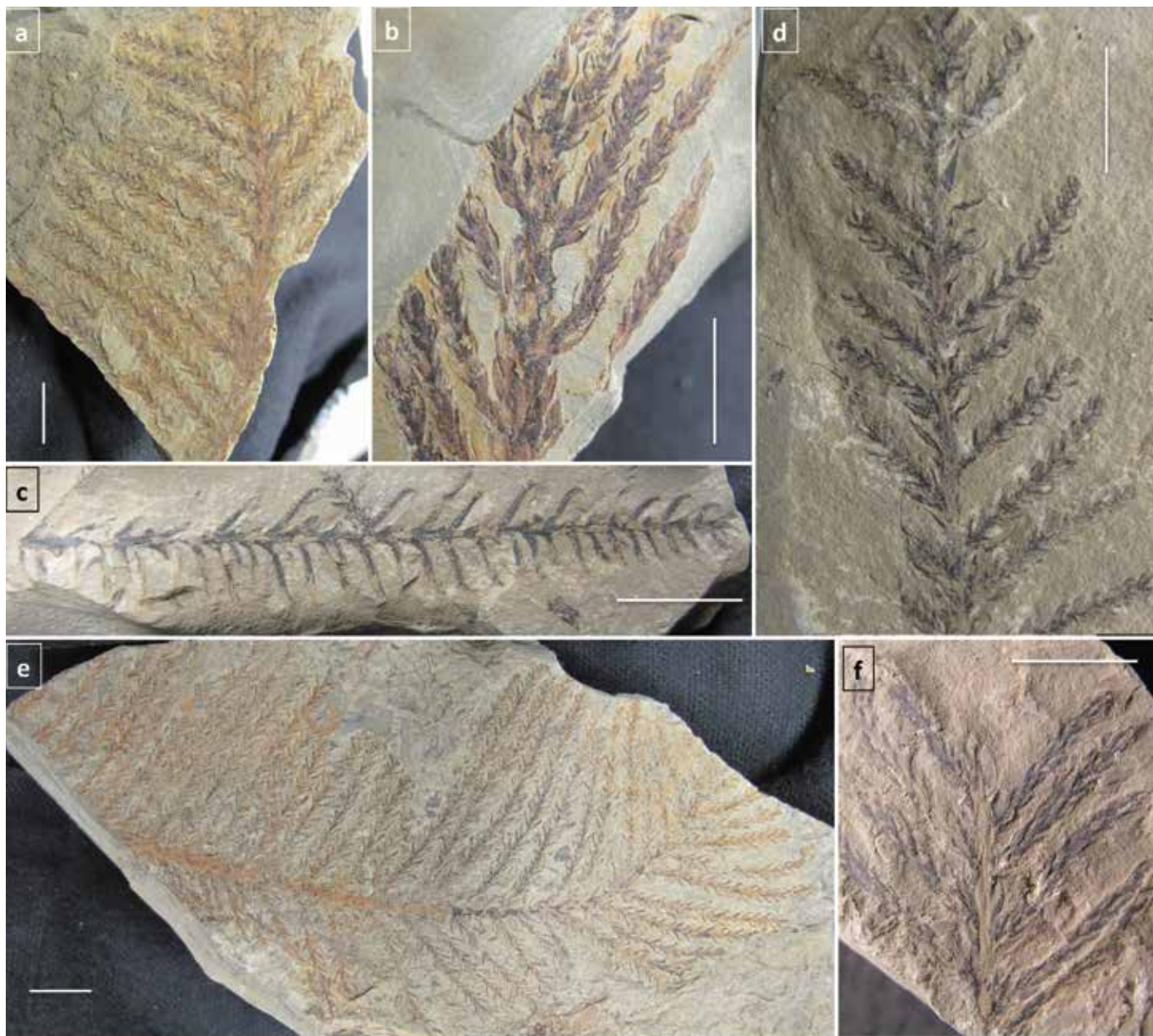


FIGURE 12. Unit 10, USGS locality 8975, walchian conifers. (a) Walchian conifer Morphotype B. USNM specimen 619025. (b) Walchian conifer Morphotype D. USNM specimen 619026. (c) Walchian conifer Morphotype D. USNM specimen 619027. (d) Walchian conifer Morphotype B. USNM specimen 619028. (e) Walchian conifer Morphotype B branch fragment. USNM specimen 619029. (f) Walchian conifer Morphotype B; however, note that the leaves are shorter and more closely adpressed to the stem than is typical of that morphotype. USNM specimen 619030. Scale bars = 1 cm.

comment below in Stratigraphic and Environmental Interpretations subsection).

Several specimens were found of elongate, strap-like foliage with parallel veins, likely of cordaitalean origin (3.7%; Figure 14o). The uniformity, consistent separation, and regular spacing of the longitudinal striations in these specimens argue for them

being veins rather than sclerenchyma strands. Thus, these specimens are likely leaves rather than pteridosperm or fern rachis fragments.

Three specimens have characteristics of the pteridosperm genus *Alethopteris*. Pinnules are relatively short and have an inclined insertion, with subparallel lateral margins and a round to

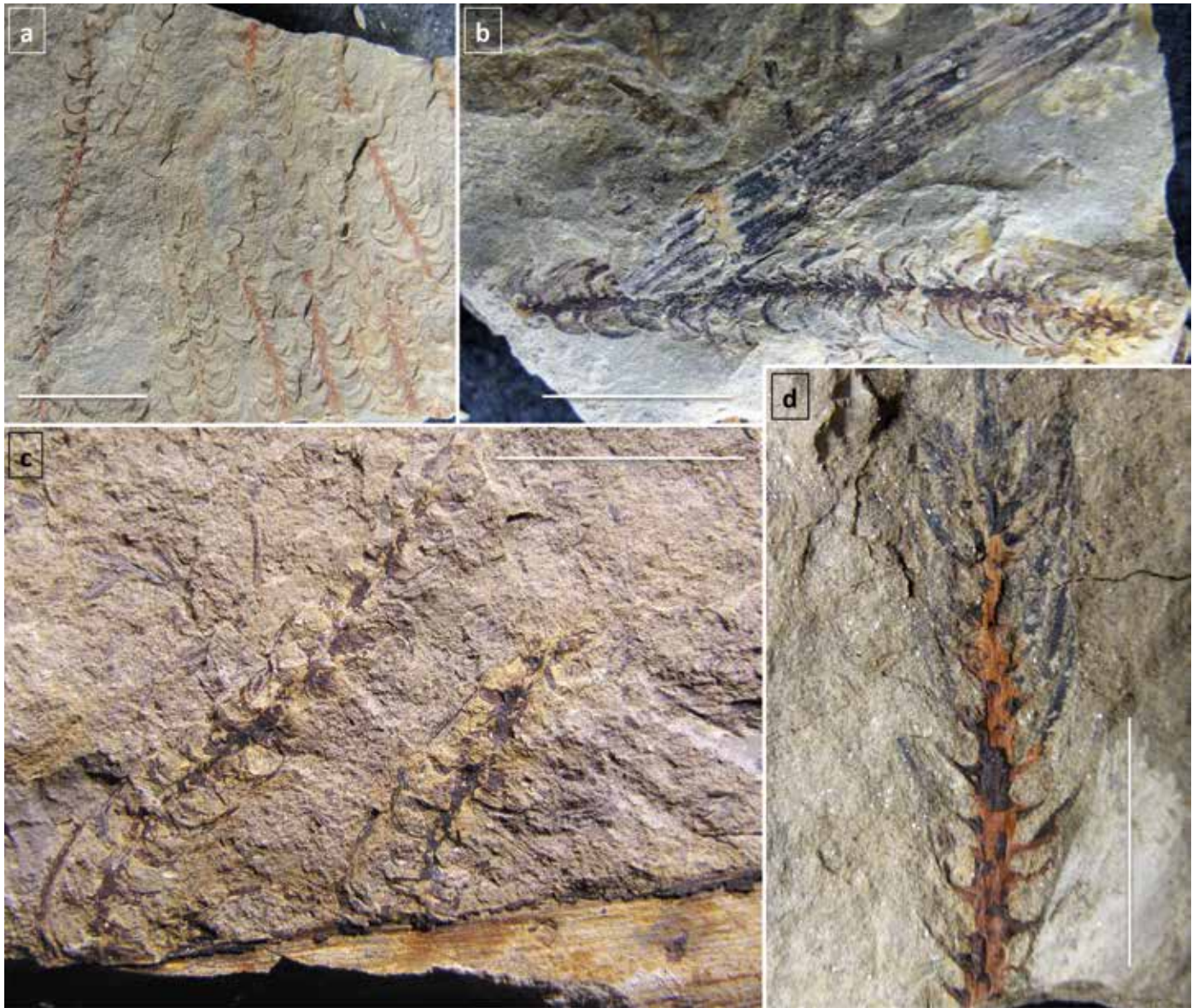


FIGURE 13. Unit 10, USGS locality 8975, conifers. (a) Walchian conifer Morphotype A vegetative branches with obliquely inserted leaves. USNM specimen 619031. (b) Walchian conifer Morphotype A with obliquely inserted leaves, apex to the left. Calamitalean stem with clearly marked node above the conifer branch. USNM specimen 619032. (c) Possible ovuliferous Walchian conifer Morphotype A. USNM specimen 619033. (d) Walchian conifer vegetative axis or, possibly, remains of a partially disaggregated ovuliferous cone. USNM specimen 619034. Scale bars = 1 cm.

bluntly pointed apex. The base of a pinnule is decurrent, but pinnules are not or are only weakly confluent. The midvein extends about $\frac{2}{3}$ of the way to the pinnule apex, and the lateral veins are not dense, arch slightly in their path, are convex to the apex, and meet the margin at an angle of $<45^\circ$. One of the specimens has an elongate terminal pinnule. We identify these specimens as most similar to *A. schneideri* (1.1%; Figure 16d–f). Another possible identification is *Alethopteris zeilleri*; in this case, the

pinnules would be expected to have somewhat denser venation, oriented more closely to orthogonal to the midvein and margins, with somewhat more bluntly acute pinnule apices and less inclined pinnule insertions. However, a clear identification cannot be made on the basis of the fragmentary material at hand.

Sphenopteris germanica (2.2%; Figure 16g–i) specimens, although not common, are well preserved and show considerable variation in form. Pinnules vary from squared off at the

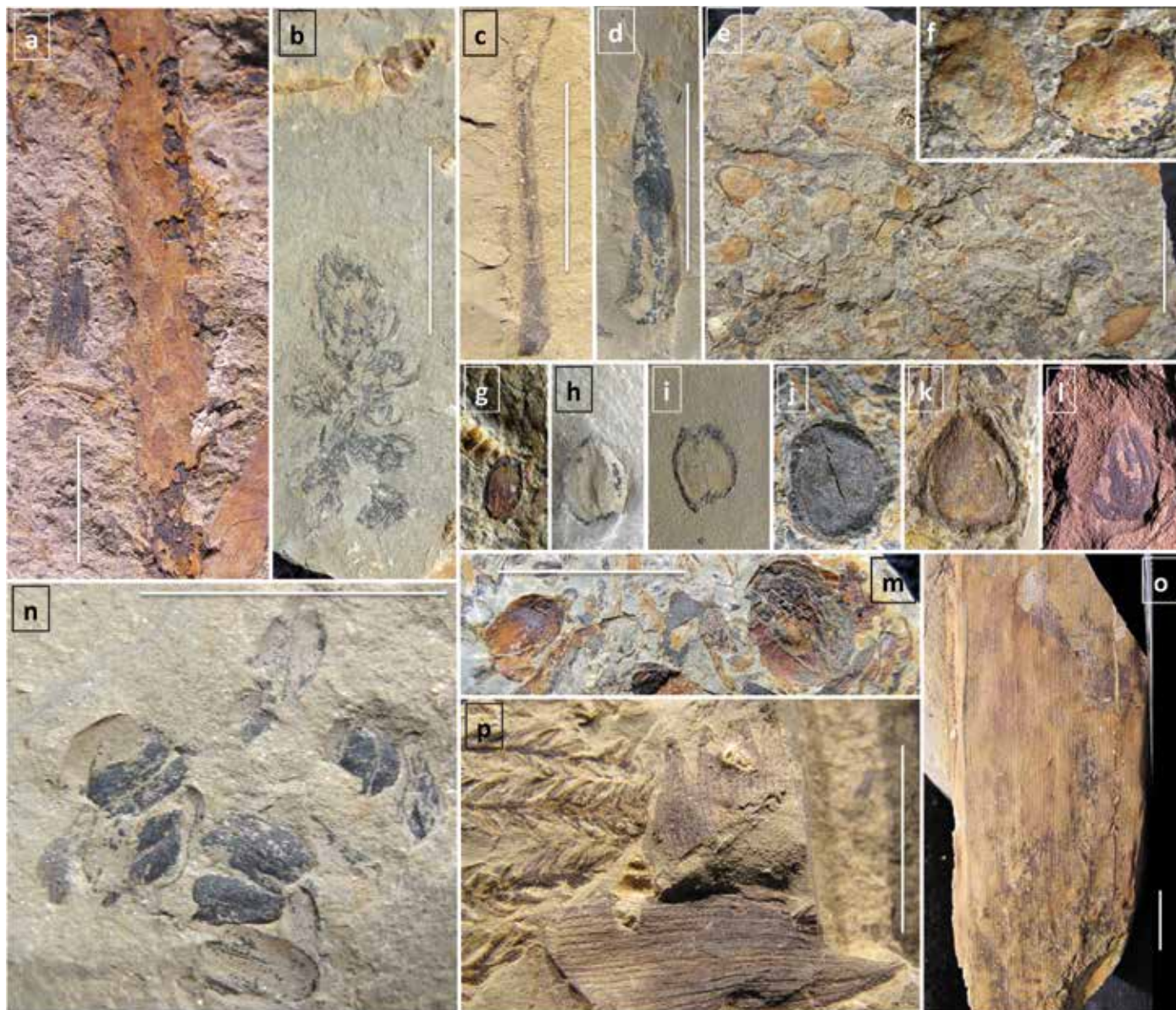


FIGURE 14. Unit 10, USGS locality 8975, various specimens. (a) Walchian conifer stem with leaves still in attachment and leaf scars where the leaves have been removed during splitting of the rock. USNM specimen 619035. (b) Walchian conifer buds or polliferous cones. Note mold of snail at top of image. USNM specimen 619036. (c) *Gomphostrobus bifidus*, bract from ovuliferous walchian cone. USNM specimen 619037. (d) Incertae sedis, possible ovuliferous conifer cone bract. USNM specimen 619038. (e) Numerous seeds of similar kind within a layer of comminuted plant debris (CPD), suggesting a synchronous reproductive event. USNM specimen 619039. (f) Close-up of seeds from the layer shown in Figure 14e. USNM specimen 619040. (g)–(l) Seeds of various shapes and sizes to demonstrate the range of seed types preserved in Unit 10 sediments. All, including image (f), are at identical magnifications. USNM specimens (g) 619041, (h) 619042, (i) 619043, (j) 619044, (k) 619045, and (l) 619046. (m) Two seeds of different morphology preserved in a CPD layer. USNM specimen 619047. (n) Valvate organs that may be pollen-producing organs shed from a more complex peltasperm reproductive structure. USNM specimen 619048. (o) Cordaitalean leaf fragment, broad, strap-like with longitudinally parallel venation. USNM specimen 619050. (p) *Charliea* sp. cf. *C. manzanitanum* leaves, at least three, the top fragment preserving the distinctive leaf tip. Scale bars = 1 cm. USNM specimen 619049. The scale bar in (m) also applies to (f)–(l).

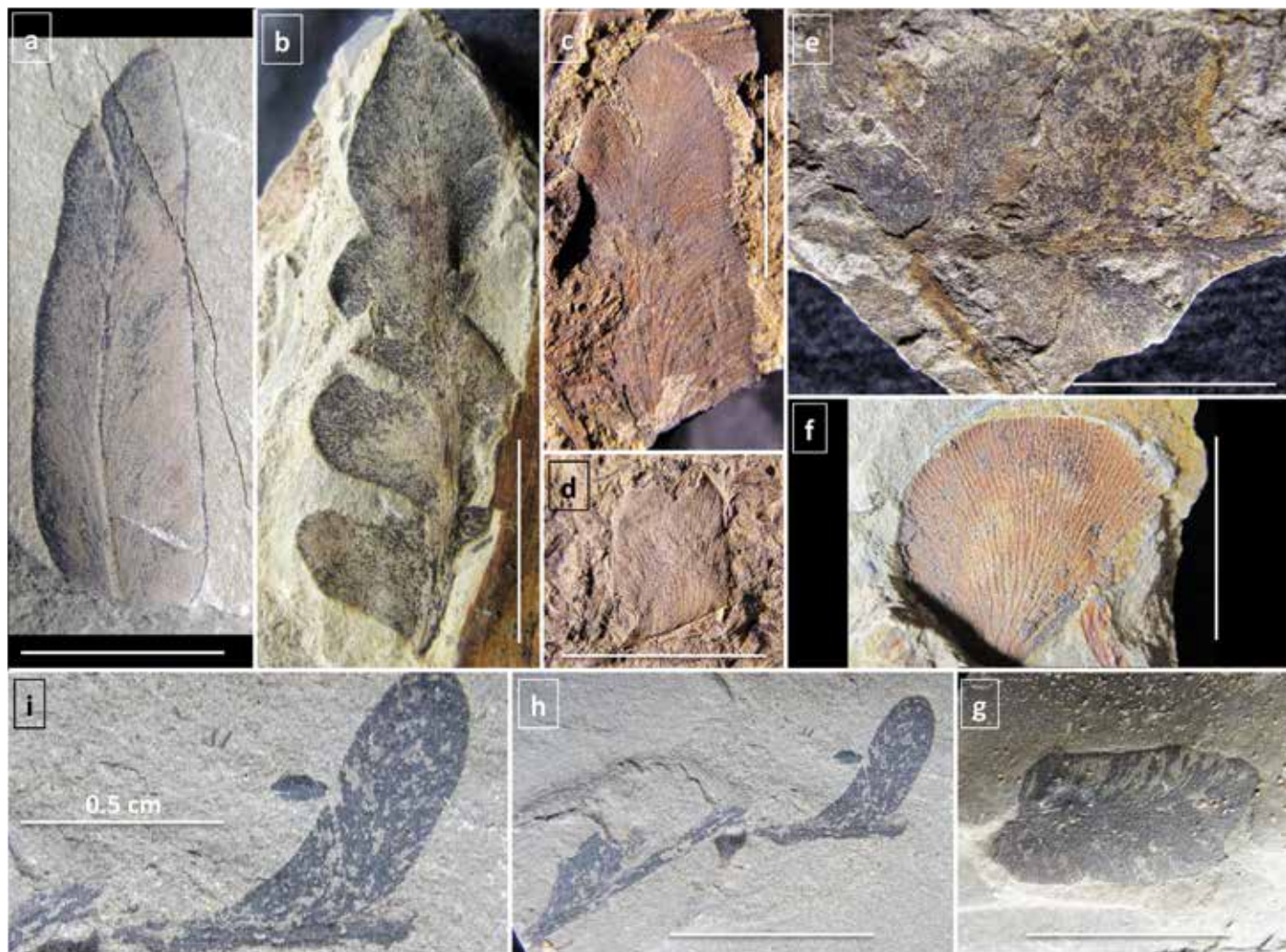


FIGURE 15. Unit 10, USGS locality 8975, seed plant foliage. (a)–(d) *Odontopteris* (*Mixoneura*) *schlotheimii*, different manifestations of pinnae showing entire laminae, individuated pinnules, and terminal pinnules where subjacent pinnules have fused. Veins are relatively widely spaced. Pinnules are angular. USNM specimens (a) 619053, (b) 619054, (c) 619055, and (d) 619056. (e)–(g) *Odontopteris* (*Mixoneura*) *subcrenulata*. Various forms of pinnule and pinna morphology. Venation is dense. Pinnules are rounded. USNM specimens (e) 619057, (f) 619058, and (g) 619059. (h) *Rhachiphyllum* sp. cf. *R. schenkii*. (i) Magnification of specimen illustrated in Figure 15h. Note the flat pinnule aspect, nonsunken midvein, and steep, straight lateral veins. USNM specimen 619060. Scale bars = 1 cm except as noted.

tips to rounded. Venation varies from prominent, with the veins strongly protruding from the lamina, to muted, where veins are difficult to identify.

Several partially preserved pinnules of indeterminate affinity but of neuropteroid aspect occur, in toto, at a frequency of nearly 6%.

Various pteridophytes also occur in the flora: Calamitaleans include stems (1.1%) (Figures 13b, 17a); a small form of *Annularia*, possibly *A. spicata* (0.7%, $n = 2$) with fusiform, relatively short leaves (Figure 17b); and a small cluster of cones similar to *Calamostachys spicata* (0.4%, $n = 1$; Figure 17c).

Two isolated sphenophyll leaves also are present (Figure 17d), identified tentatively as *Sphenophyllum thonii* (0.7%) on the basis of rounded distal leaf margins that grade into the lateral margins, both of which are lined by small teeth and by veins that terminate along the lateral margins rather than strictly at the distal margin. Given the intraspecific variation in *Sphenophyllum* leaves, identifying isolated leaves often must be tentative. Possibilities include *Sphenophyllum verticillatum* and *Lilpopia raciborskii* (see comparisons in Kerp, 1984; Wagner, 1985; Barthel, 2009).

The ferns include both groundcover and tree fern foliage, and all specimens are rare. The small fern *Oligocarpia gutbieri*

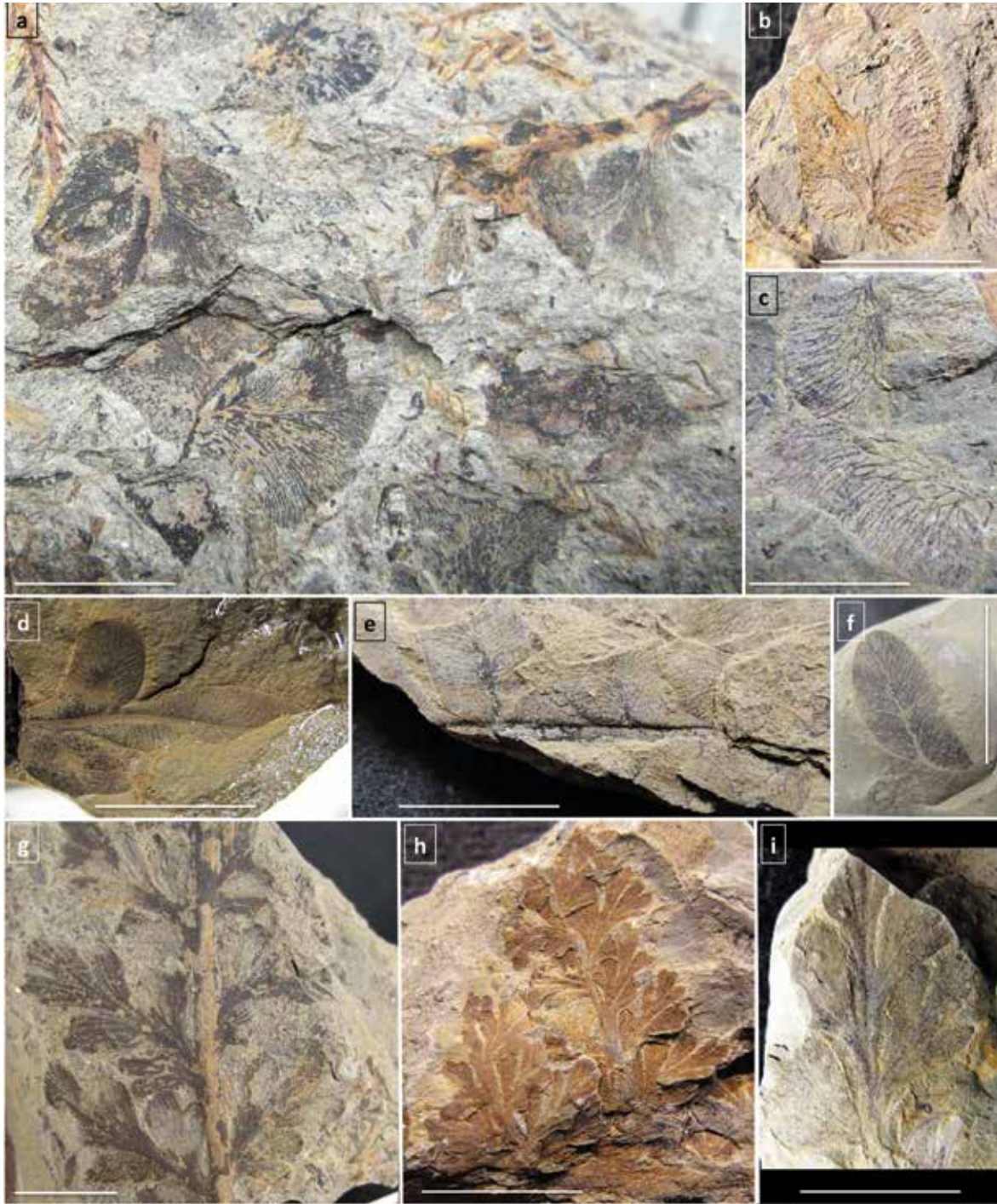


FIGURE 16. Unit 10, USGS locality 8975, various specimens. (a) *Odontopteris* (*Mixoneura*) *subcrenulata*. Fragments of several pinnae. Mixed with walchian conifer fragments. USNM specimen 619061. (b)–(c) Pinnules with reticulate venation. Compare with *Reticulopteris muensteri* or undescribed species. USNM specimens (b) 619062 and (c) 619063. (d)–(f) *Alethopteris* sp. cf. *A. schneideri*. Relatively short, broad pinnules with bluntly rounded tips, weakly confluent, deeply incised apical attachment. USNM specimens (d) 619064, (e) 619065, and (f) 619066. (g)–(i) *Sphenopteris germanica*. Note variability in the shape of pinnule lobes and the prominence of the venation. USNM specimens (g) 619067, (h) 619068, and (i) 619069. Scale bars = 1 cm.

(2.2%; Figure 17i–k) has rounded pinnules, differentiating it from *O. leptophylla*; flexuous rachises; and widely spaced, relatively flexuous pinnule venation. *Sphenopteris* sp., with small pointy pinnule lobes, similar to *S. biturica* or *S. mathetii*, also likely a small, filicalean fern, was present in one quadrat (0.4%). Two forms of marattialean tree fern foliage were identified; one is similar to *Lobatopteris geinitzii* (0.7%, $n = 2$; Figure 17f), and the other, identified by Read (note in collection drawer) as *Pecopteris oreopteridia*, is here identified as more similar to *Pecopteris densifolia* (0.7%, $n = 2$). A large flabellate leaf may be a pecopterid aphlebia (0.4%, $n = 1$; Figure 17h, but see below for further comment).

Noeggerathialeans are represented by a single specimen of *Charliea* sp. cf. *C. manzanitanum* (0.4%, $n = 1$; Figure 14p). Several pinnules are present, one with the distinctive division of the leaf terminal margin into three pointed, toothlike lobes and all with strongly parallel pinnule venation.

Unidentifiable material, or plant remains not specifically attributable to a rank of order or below, includes several coarsely veined, flabellate objects, possibly aphlebiae or cyclopterid fragments. It is difficult to provide a definitive identification of these objects because of their fragmentary preservation. One of these, similar to a marattialean aphlebia (Figure 17h), also is similar to more typically Angaran foliage, such as *Psymophyllum* (see Naugolnykh, 1998). The other form, represented by several fragmentary specimens (1.1%; Figure 17m), has dense, fine veins that spread outward in a palmate manner from the base, which appears to be an entry point for multiple veins. Such specimens have no clear affinities to which the authors can point. A final odd object (Figure 17e) is a small, planar, leaflike or cone-scale-like structure with strongly developed, pointed terminal teeth and a wide vein ending in each tooth (0.4%, $n = 1$). The overlapping nature of what appear to be lobes, their large number, and pointed distal teeth suggest walchian cone-scale affinities.

Seeds of various morphologies (Figure 14e–m) are common in this collection (19%), more so than in any of the other Abo Canyon collections; this may reflect the abundance of CPD (25.3%) in which many of the seeds were found. Indeterminate axes include striate specimens, presumably from pecopterid ferns or pteridosperms (9.3%), and woody axes from conifers or other large plants (3.7%).

STRATIGRAPHIC AND ENVIRONMENTAL INTERPRETATIONS

The Unit 10 flora is the largest and most diverse of the floras in the Read Abo Canyon collection suite. Considered in toto, the composition of the flora suggests strong seasonality at the time of plant growth and during the burial of the plant remains. This is indicated by conifer dominance and the presence of pteridosperms such as the mixoneurid *Odontopteris*, *Rhachiphyllum*, and the reticulate-veined cf. *Reticulopteris* sp. and by plants that occur only in association with other plants and sedimentological indicators of periodic drought, such as *Charliea*. However, some of the rarer elements of the flora indicate the at least local

presence of wet substrates, including calamitaleans and marattialean tree ferns, which occurred during the Pennsylvanian and early Permian almost anywhere that some form of standing water was available. The flora also includes small, groundcover ferns and sphenophylls, indicating that the environment was not arid.

The animal fossils in close association with the plant remains, particularly spirorbids attached to probable floating material, suggest a coastal or estuarine depositional environment. Furthermore, the abundance and dense, thick concentrations of comminuted plant debris; abundant muscovite, often concentrated in layers; and the lack of distinctive indicators of scour or rapid deposition of the larger plant remains (absence of remains crossing bedding planes, jumbled within the sediment, or aligned by flow) are consistent with deposition of the plants in a quiet-water setting into which sediment and organic matter were introduced episodically. This interpretation is further supported by the large number of quadrats lacking organic matter, which indicates episodic introduction of organics.

Interpretation of the age of this flora is complicated by its strongly dryland affinities. The difficulties in determining the age of such assemblages from plant composition alone are indicated, perhaps in an extreme example, by the study of van Hoof et al. (2013), in which a conifer-rich flora thought to be of Permian age was shown to be Middle Pennsylvanian. In the case of Unit 10, the flora is unproblematically Late Pennsylvanian, most likely Missourian. The presence of a reticulate-veined medullosan of uncertain affinity but similar to Middle Pennsylvanian *Reticulopteris* (Figure 16b,c) is noteworthy. Neither the survival of *Reticulopteris* into the Late Pennsylvanian of western Pangea nor the evolution of a convergent form can be ruled out on the basis of the specimens at hand. Further, although the evidence is too slim for a confident age correlation, isolated pinnules with shape and venation similar to those from Abo Pass have been identified east of Socorro, New Mexico, from strata of the Tinajas Member of the Atrasado Formation (DiMichele, Kerp, Lucas, and Chaney, unpublished data); these strata are confidently dated as late Missourian in age on the basis of conodonts (Lucas et al., 2013; see their fig. 15.1 for a photograph of the outcrop on which the fossiliferous bed is marked by a white arrow).

In terms of the regional stratigraphy, on the basis of the above considerations this assemblage probably was collected from the upper part of the Atrasado Formation. We suspect it is drawn from the Read and Wood (1947) “upper arkosic member of the Madera Formation” (Figure 2). This location would most likely place it near the Missourian–Virgilian (Kasimovian–Gzhelian) boundary, although we cannot suggest further refinement.

UNIT 35

Unit 35 is USGS locality 8976. The hand specimens consist of tan-colored, micaceous siltstone. Thin concentrations of muscovite flakes drape thicker layers of siltstone (~1 cm), suggesting periodicity of water flow velocity, with muscovite concentrating



FIGURE 17. Unit 10, USGS locality 8975, minor elements. (a) Calamitalean stem with node. USNM specimen 619071. (b) *Annularia* sp. cf. *A. spicata*. Leaves are the correct, fusiform shape for this species but are somewhat larger than is typical. USNM specimen 619072. (c) *Calamostachys spicata*, calamitalean cones. USNM specimen 619073. (d) *Sphenophyllum* sp. cf. *S. thonii*. USNM specimen 619074. (e) Incertae sedis, possible coniferous cone scale. USNM specimen 619070. (f) *Lobopteris geinitzii*, marattialean fern foliage. USNM specimen 619210. (g) *Pecopteris densifolia*, marattialean fern foliage. USNM specimen 619211. (h) Incertae sedis, flabellate organ, possibly a marattialean aphlebia or a fragment of a plant of exotic affinity (see text). USNM specimen 619212. (i)–(k) *Oligocarpia gutbieri*, frond fragments. Note flexuous rachises, rounded pinnules, and widely spaced venation with weak midvein development. USNM specimens (i) 619213, (j) 619214, and (k) 619215. (l) *Peltaspermum*-like reproductive organ. USNM specimen 619216. (m) Incertae sedis, flabellate organ, possibly leaf of exotic affinity. USNM specimen 619217. Scale bars = 1 cm.

during slack-water periods. Plant remains are often somewhat aligned and thickly disposed on bedding surfaces; they appear to have been allochthonous. The plants are uniformly scrappy, and comminuted plant debris is common. As in other Abo Canyon plant deposits, charcoal is rare, noted in this collection only on a single sampling quadrat. No animal fossils were noted, distinguishing this collection from all others except those from the Abo Formation.

FOSSIL FLORA

The flora of Unit 35 has a more Pennsylvanian wetland aspect than any other of the Read Abo Canyon collections, particularly when considered quantitatively and at the generic level. However, it also bears a strong imprint of seasonal moisture limitation and can be characterized as a mixed flora. There is no evidence that the plants generally considered typical of drier substrates were transported from uplands and mixed with the litter of lowland vegetation. Preservation of all taxa is about the same quality and type, indicating local transport, but not of such turbulence that all organic matter was obliterated.

Pteridosperms dominate the flora, followed by walchian conifers, calamitaleans, and pecopterid ferns. The equally most abundant taxa are *Macroneuropteris scheuchzeri* and walchian conifers, followed in descending order by calamitaleans, neuropterids (represented by numerous isolated pinnules), *Sphenophyllum oblongifolium*, *Odontopteris brardii*, and marattialean tree ferns. Consequently, there is a significant pteridophyte component to the flora, greater numerically than in any of the other collections.

Macroneuropteris scheuchzeri is the most abundant pteridosperm in the flora (17.8%). This distinctive species is easily recognized by its large, linguloid pinnules with a thin midvein that extends the length of the pinnule and dense, arching lateral veins (Figure 18a and possibly 18b). Examined in detail, many specimens have small “hairs” that appear to be on the leaf surface (Figure 18c, at arrows), although Laveine and Oudoire (2015) have suggested that these, in fact, are subepidermal resin ducts.

Walchian conifers are of equal importance to *M. scheuchzeri* in abundance (17.8%). Two forms were identified. The most common form (Figure 18e) has shoots bearing leaves that were bilaterally flattened and strongly directed acroscopically but concave in curvature, held some distance off the stem, and with tips that recurve toward the apex; these shoots are most like Morphotype B. The less common form has leaves that are borne at about a 40° angle to the stem, are nearly straight and narrow (not wide bilaterally), and turn upward at the tips (Figure 18d); these specimens conform, more or less, to Morphotype D.

Sphenopteris germanica (Figure 19a) occurs at a frequency of 11.9%, making it the third most abundant plant in the collection. As in other Abo Pass collections, *S. germanica* specimens are fragmentary. They show the three- to five-lobed pinnules with coarse, sparse venation. Pinnule lobes are spatulate and have rounded to nearly flat outermost margins.

The third most common group of pteridosperms is those attributable to the genus *Odontopteris*, including those forms sometimes attributed to *Mixoneura*. The most common of these (10%) is *O. brardii* (Figure 19b,c), characterized by elongate, triangular pinnules with a weak midvein and multiple veins entering pinnule lamina from the supporting rachis. The pinnule margins may appear to be slightly undulate at the points where veins end, but this characteristic is not universal and may reflect the effects of natural maceration prior to burial. Rare elongate pinnules (5% of quadrats) with dense, relatively coarse venation and marginal undulations (Figure 19d) may be terminal portions of *O. brardii* pinnae; however, these also may be attributable to *O. subcrenulata*, among other possibilities.

Three specimens (3%) of odontopterid aspect have widely spaced veins in the preserved pinnule fragments (Figure 19e–g). Pinnules have weak midveins and steep lateral veins with multiple veins entering the base of a pinnule (Figure 19e,f). In other instances, the margin of the pinnule/pinna may be undulatory but otherwise of odontopterid aspect, with widely spaced, fine veins (Figure 19g). The specimen illustrated in Figure 19g also may be of this type, but being apical, marginal undulations are muted. We attribute these specimens to *Odontopteris* (*Mixoneura*) *schlotheimii*.

As noted above, at least 5% of odontopteroid specimens are elongate, lingulate laminae with dense lateral veins. These specimens may be attributable to *Odontopteris* (*Mixoneura*) *subcrenulata*. Two are illustrated (Figures 18b, 19d). The specimen illustrated in Figure 18b can be compared to the *Macroneuropteris scheuchzeri* specimen illustrated next to it in Figure 18a. The possible *O. subcrenulata* pinna has much straighter secondary veins that turn up sharply as they come into contact with the margin, whereas those of *M. scheuchzeri* arch through the lamina.

A single, large cyclopterid-like pinnule was found (Figure 20d), which may belong to *Odontopteris brardii* or *O. subcrenulata*. It has dense, relatively straight veins and a slightly undulatory margin.

Rare pteridosperm taxa, each represented by a single, fragmentary specimen, include *Alethopteris* sp. cf. *A. virginiana*, *Pseudomariopteris cordato-ovata*, and the callipterid *Autunia naumannii*. *Alethopteris virginiana* may be conspecific with and supersede the name *A. leonensis* (Wagner and Lyons, 1997; Blake and Gillespie, 2011). The single specimen illustrated here (Figure 20a) is similar in having somewhat triangular pinnules with little confluence with adjacent pinnule bases. Venation is obscure but can be seen to be of alethopteroid aspect. Characteristic aspects of *Pseudomariopteris cordato-ovata* seen in the Unit 35 specimen (Figure 20b) include pinnules with thick laminae, which obscure secondary venation; a prominent, slightly sunken midvein; broad pinnule bases constricted on both the acroscopic and basiscopic sides; and spinelike prolongation of the pinna tip, consistent with an inferred vine-like habit for the species of this genus, which may be of callistophytalean affinity (Krings and Kerp, 2000). The attribution of a small foliage fragment to



FIGURE 18. Unit 35, USGS locality 8976, dominant elements. (a) *Macroneuropteris scheuchzeri* pinnule fragment. Note possible insect marginal feeding damage at upper right, including reaction rim. USNM specimen 619218. (b) *Macroneuropteris scheuchzeri* or *Odontopteris* (*Mixoneura*) *subcrenulata* pinnule. Differences discussed in text. USNM specimen 619220. (c) *Macroneuropteris scheuchzeri* pinnule tip with distinctive “hairs” (at white arrows), which may be subepidermal resin canals. USNM specimen 619219. (d) Walchian conifer Morphotype B, slightly different in leaf shape, angle of insertion, curvature of the lamina. USNM specimen 619221. (e) Walchian conifer Morphotype B. USNM specimen 619222. Scale bars = 1 cm.

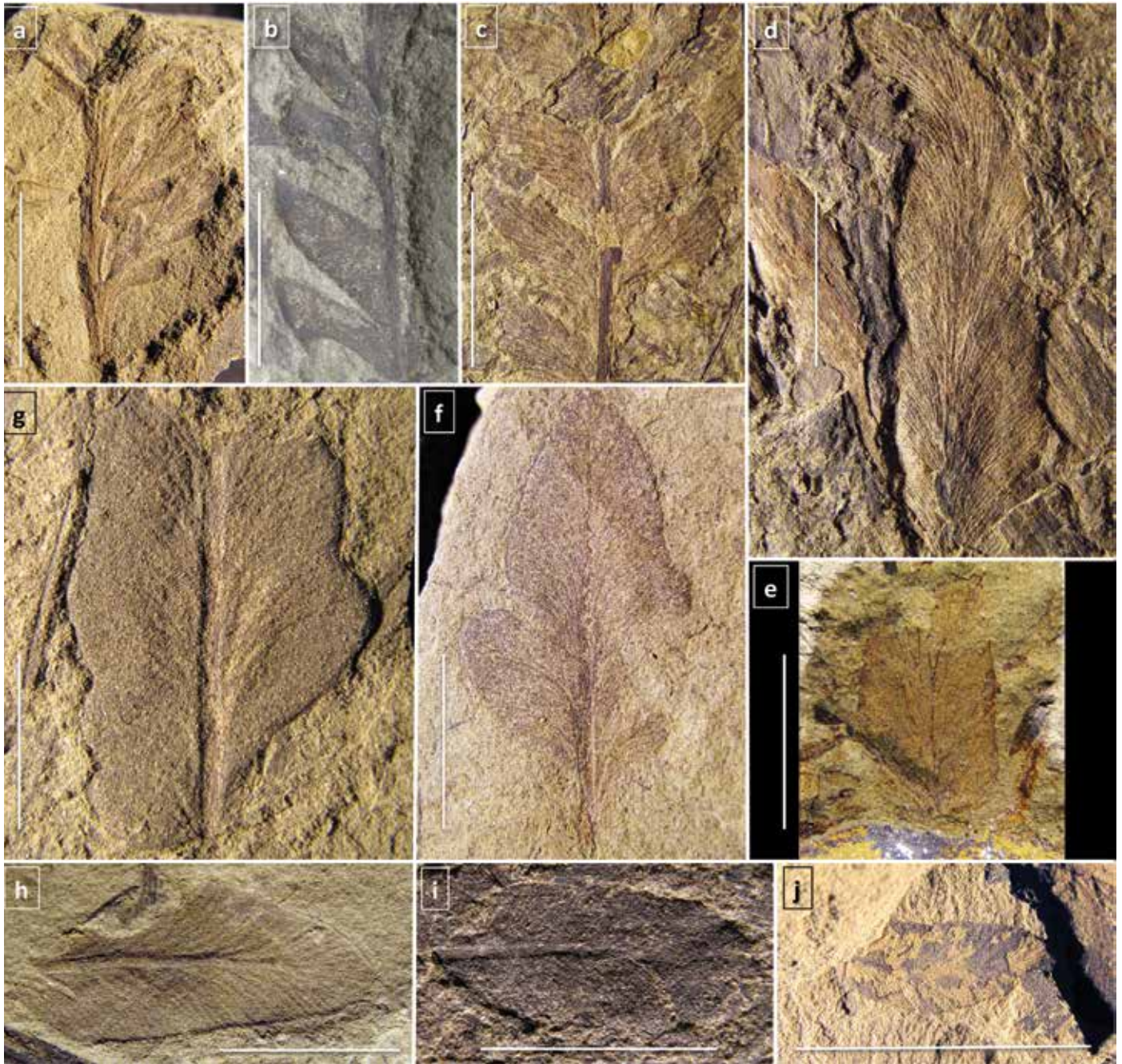


FIGURE 19. Unit 35, USGS locality 8976, subdominant elements. (a) *Sphenopteris germanica*. USNM specimen 619223. (b)–(c) *Odontopteris brardii*. USNM specimens (b) 619224 and (c) 610225. (d) *Odontopteris brardii* or *Odontopteris (Mixoneura) subcrenulata* terminal pinnule/pinna. USNM specimen 619226. (e)–(g) *Odontopteris (Mixoneura) schlotheimii*. Several pinnules or pinnae with widely spaced lateral veins, high-angle secondary venation, and angular free pinnule shape. USNM specimens (e) 619227, (f) 619228, and (g) 619229. (h) Pinnule fragment most closely resembling *Odontopteris (Mixoneura) schlotheimii*. USNM specimen 619230. (i) Pinnule fragment most closely resembling *Odontopteris (Mixoneura) schlotheimii*. USNM specimen 619321. (j) Pinnule fragment most closely resembling *Pecopteris*. USNM specimen 619232. Scale bars = 1 cm.

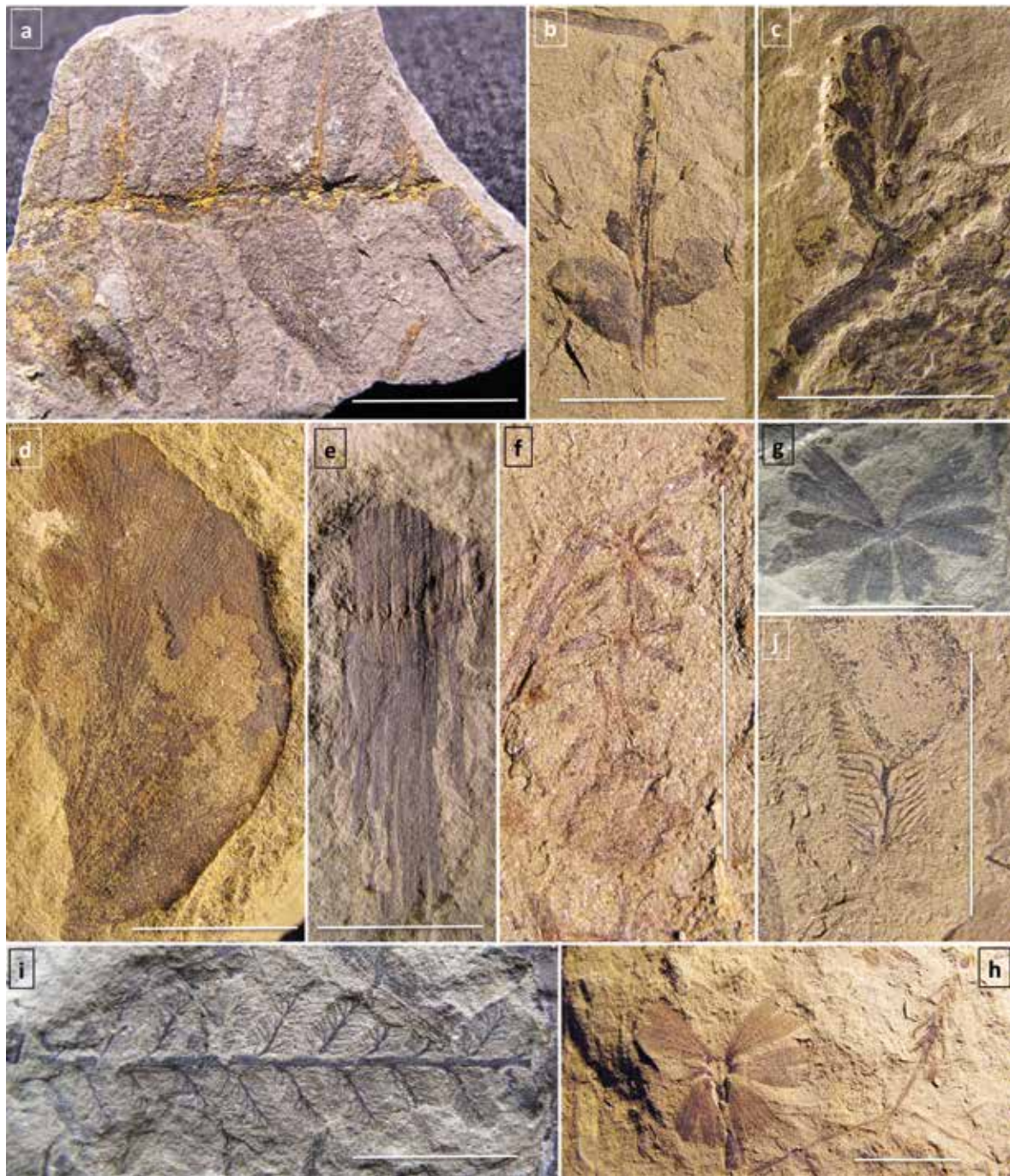


FIGURE 20. Unit 35, USGS locality 8976, minor elements. (a) *Alethopteris virginiana*. USNM specimen 619242. (b) *Pseudomariopteris cordato-ovata*. Note spinelike prolongation of the pinna tip. USNM specimen 619243. (c) *Autunia naumannii*. USNM specimen 619244. (d) Cyclopterid pinnule, possibly of *Odontopteris brardii* or *Odontopteris (Mixoneura) subcrenulata*. USNM specimen 619245. (e) Calamitalean stem with node. USNM specimen 619246. (f) *Annularia spicata*. USNM specimen 6192467. (g) *Sphenophyllum oblongifolium*. USNM specimen 619248. (h) *Sphenophyllum oblongifolium* and walchian conifer. USNM specimen 619249. (i) *Polymorphopteris (Acithea) polymorpha* marattialean fern pinna. Venation not fully developed in each pinnule. USNM specimen 619251. (j) *Polymorphopteris polymorpha* pinnule. USNM specimen 619250. Scale bars = 1 cm.

Autunia naumannii (Figure 20c) is suggested by its lobed, undulate lamina and small size. However, any identification of such a small fragment must be considered tentative. It is possible that it represents an isolated pinnule/pinna of *Sphenopteris germanica*, although it is quite small for that and has a larger number of pinnule lobes than would be expected.

Sphenopsids in the flora include both calamitaleans and sphenophylls. The calamitaleans include both stem material (Figure 20e; 9.9%) and two foliage species, both attributable to *Annularia*. One, *A. spicata*, is quite small (Figure 20f; 7.9%), composed of whorls of narrow, short leaves of fusiform shape, similar to *A. spicata* var. *eimeri* of Remy and Remy (1975; see also specimens illustrated by Kerp and Fichter, 1985). A single specimen with large, spatulate leaves in ovoid whorls is attributed to *A. carinata*.

Two forms of sphenophylls occur in the assemblage. Most of these (11.9% of all quadrats) are attributable to *Sphenophyllum oblongifolium* (Figure 20g,h), typified by six leaves per whorl, with two pairs borne opposite to one another and the third, generally of shorter leaves, borne at right angles below the two pairs. A smaller number of specimens (5% of all quadrats) consist of isolated, small, triangularly shaped leaves with small blunt teeth along the outer margin, possibly attributable to *S. verticillatum*.

Ferns are common components of the flora of Unit 35, most of marattialean tree fern affinities. However, small scraps of what are likely filicalean ferns also were found.

Marattialean tree fern foliage is notoriously difficult to identify in fragmentary preservation, in part because of high intrafrond morphological variability and in part because of oversplitting taxonomically. Marattialean foliage in the collection (approximately 14% frequency) is largely fragmentary and has been identified only as *Pecopteris* sp. (a name that Cleal, 2015, recommends abandoning for marattialean foliage for taxonomic reasons, and although taxonomically correct, at the present time there is no substitute for this long-used name). Some foliage fragments (Figure 20i,j), however, have venation characteristic of *Polymorphopteris* (*Acithea*) *polymorpha* (Wagner, 1959; Zoderow et al., 2006), in which the lateral veins first branch close to the pinnule midvein and then each limb of the initial fork may branch again to form a symmetrical pair of forked veins.

Small ferns are represented only by tiny fragments of material found among the comminuted plant debris. The most common of these (5% of all quadrats) has small rounded pinnules with weakly differentiated midveins; widely spaced, ascending, dichotomous venation; and a somewhat flexuous rachis (Figure 21g). Were these of larger size, they might be attributed to *Oligocarpia* sp. cf. *O. gutbieri*, although *O. leptophylla* is also a possibility. A single, tiny terminal portion of a pinna is attributable to *Sphenopteris* sp. cf. *S. biturica* (see Wagner, 1985) or *S. mathetii* (see Barthel, 2009). Another single specimen can be designated only as *Sphenopteris* sp. (Figure 21h), although it may be a very small specimen of *Oligocarpia*.

Lycopsids are represented in the Abo Canyon collection only in the Unit 38 flora. These include a number of specimens but none that point clearly to whole-plant taxa or that are sufficient to give an indication of the diversity of these plants on the landscape. Three small-stem specimens (two illustrated in Figure 21a,b) may be some kind of isoetoid with an upright stem and permanently attached short leaves. The leaves are widely spaced and helically arranged in both specimens; apparent leaf scars are the result of fracture of the specimens during splitting of the encasing rock matrix. The leaves are too short to conform to known species of small isoetaleans, such as *Polysporia* (Chaloner, 1958), but this kind of lycopsid has rarely been noted in descriptions of fossil floras. Small specimens of *Lepidostrobophyllum*, perhaps *L. hastatum*, are characterized by a distinctly triangular distal lamina and a short, keeled proximal lamina (Figure 21d,e). Three of these were found in the collection. They are from a small cone of a heterosporous lycopsid, one that produces deciduous sporangium-sporophyll units and thus likely produced a single functional megaspore. They suggest the presence of tree lycopsids of the Diaphorodendraceae or Lepidodendraceae. Finally, two fragments of suspect lycopsid leaves, *Lepidophylloides*, were found (Figure 21c); these are of the typically long, narrow, grasslike form with a single central midvein.

Final components of the flora include small, isolated pinnules of various sizes, mostly fragmentary, thus making specific and even generic identification impossible. It is likely that many, even most, such specimens are not neuropterids; some may be marattialean fern foliage (e.g., Figure 19j), others *Odontopteris* (e.g., Figure 19h and perhaps 19i). In total, these occur on 14.8% of all fossiliferous quadrats. Seeds (e.g., Figure 21i) are common but not abundant, occurring on approximately 10% of quadrats. The most common plant remains in the assemblage are striate axes, likely from either pteridosperms or marattialean tree ferns, which have an occurrence frequency of 70.3%. Small roots were noted on 11.9% of quadrats, suggesting postdepositional rooting of the sediment (the roots do not appear to have been washed in with the aerial litter).

STRATIGRAPHIC AND ENVIRONMENTAL INTERPRETATIONS

The Unit 38 flora contains few taxa diagnostic of stratigraphic location. Most of the species-level taxa are long ranging and cross through the Middle–Late Pennsylvanian boundary. The most that can be said with confidence is that the flora is either late Middle Pennsylvanian or Late Pennsylvanian, probably Missourian. The presence of *Sphenophyllum oblongifolium* is considered diagnostic for that time interval and is not known to occur earlier (Blake et al., 2002; Wagner and Álvarez-Vázquez, 2010), setting a lower boundary to somewhere in the middle Desmoinesian. If the identification of a specimen as *Sphenopteris biturica*/*S. mathetii* is correct, it would indicate a middle Late Pennsylvanian age (Wagner and Álvarez-Vázquez, 2010), but it seems overly speculative to base an age determination on such

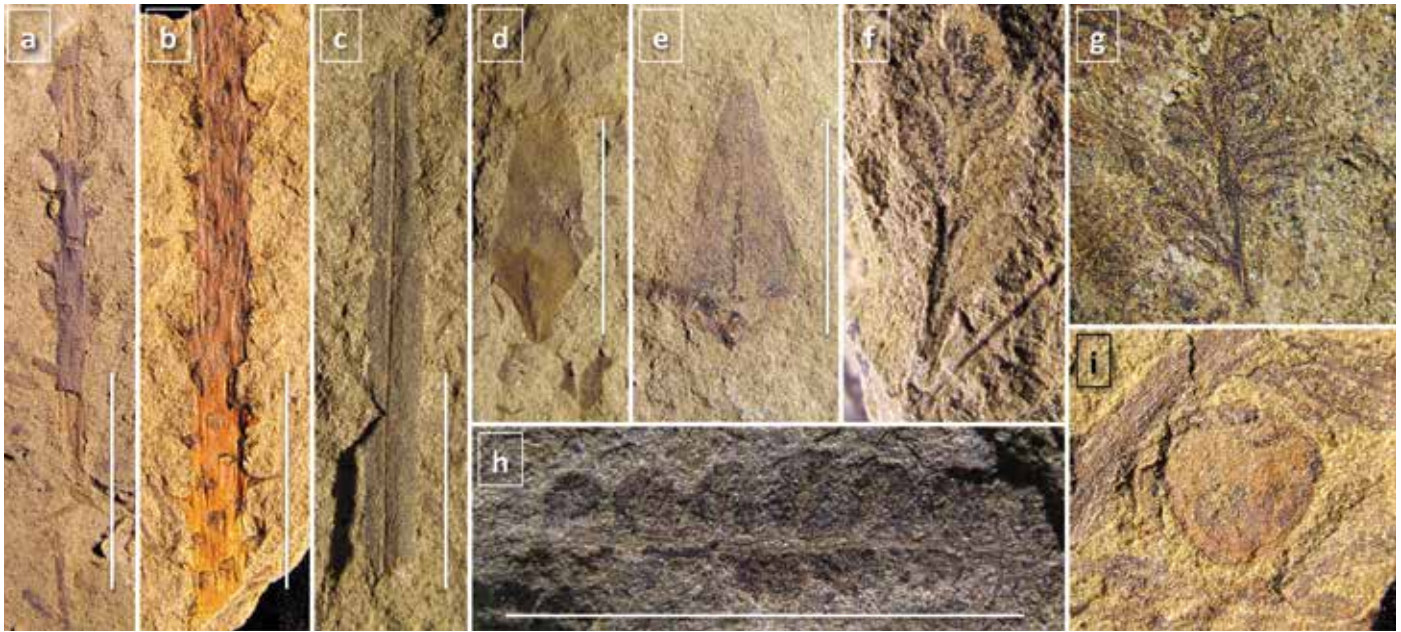


FIGURE 21. Unit 35, USGS locality 8976, minor elements. (a)–(b) Stems, possibly of small lycopsids of uncertain affinity. USNM specimens (a) 619233 and (b) 619234. (c) *Lepidophylloides*, leaf of an arborescent lycopsid. USNM specimen 619235. (d)–(e) *Lepidostrobophyllum* sp. cf. *L. hastatum*, dispersal units of megasporangiate (female) cones. USNM specimens (d) 619236 and (e) 619237. (f) *Sphenopteris* sp. cf. *S. biturica* filiclean fern foliage. USNM specimen 619238. (g) Possible foliage of *Oligocarpia gutbieri* but too minute for a confident identification as that species. USNM specimen 619239. (h) *Sphenopteris* sp. USNM specimen 619240. (i) Seed of indeterminate affinity. USNM specimen 619241. Scale bars = 1 cm. Scale bar in (h) applies also to (f), (g), and (i).

a scrap. A confounding factor for a middle Late Pennsylvanian age is the presence of lycopsid remains such as *Lepidostrobophyllum hastatum*. Although this species is long ranging, into the Late Pennsylvanian in Europe, its likely source plants in the Diaphorodendraceae sensu DiMichele and Bateman (1996) are not known to extend beyond the Middle Pennsylvanian in North America, although they do so in western Europe and in China (Wagner and Talens, 1985; Wang, 2004), and survival in more peripheral areas of the western Pangean equatorial region cannot be ruled out without better, independent stratigraphic placement.

The flora of Unit 38 is a mixture of plants with different substrate moisture preferences. Some are characteristic of high substrate moisture, such as calamitaleans, tree ferns, and the pteridosperm *Macroneuropteris scheuchzeri* (Stull et al., 2012). Others are characteristically drawn from what are often inferred to be mesic but seasonally dry settings, such as the odontopterids and mixoneurids (Rees et al., 2002; Ziegler et al., 2002; Šimůnek and Martínek, 2009), whereas others are considered to be indicators of more strongly seasonally dry settings, such as the conifers (DiMichele and Aronson, 1992; Šimůnek and Martínek, 2009; Opluštil et al., 2013). This kind of mixture is often

attributed to vegetational zonation on a landscape, reflective of soil drainage (e.g., Dimitrova et al., 2011). In principle, we agree with this interpretation. However, we would not attribute the floristic composition to long-distance transport of the more xeric elements from uplands, an interpretation that suggests soil-moisture restrictions result from drainage alone, under an otherwise generally mesic to humid climate. This interpretation, in effect, sets the default climate at the wet end of the spectrum.

Rather, the taphonomic setting of these plant remains and of most mixed floras suggests that all plants were growing in the immediate area under a climate that was seasonally dry, but with sufficient moisture to create and support patches of wetlands or corridors where the most robust wetland taxa could survive, even through periodic intervals of reduced rainfall. Thus, we believe the presence of dryland plants, so rare within stratigraphic sequences of the Pennsylvanian coal measures but present in these western Pangean basins as part of floras that are compositionally and sedimentologically distinct from the wetland floras (e.g., Galtier et al., 1992; Falcon-Lang et al., 2009; Plotnick et al., 2009; Bashforth et al., 2014, 2016), calls for setting the default climate at the dry end of the spectrum represented by the plant groups

that are present. The remainder of the flora indicates a heterogeneous landscape of the kind that is more typical of settings with seasonal rainfall than of strongly humid to perhumid climates.

DISCUSSION

In this work we have examined a stratigraphic sequence of five Pennsylvanian through Permian age floras collected in Abo Canyon, primarily by Charles B. Read of the U.S. Geological Survey in 1940 and 1941. Because Read's field notes, which are referred to on handwritten notes stored with the collections themselves, are lost or not available, we have had to determine for ourselves the most likely temporal order of these floras. However, from a combination of Read's bed-numbering scheme, notes in the collections, and the composition of the floras, the correct stratigraphic order seems apparent.

Three of the floras are arguably of Pennsylvanian age, most likely from Missourian and perhaps Virgilian strata (Kasimovian and Gzhelian). These are floras from Read's Units 38, 10, and 8 in ascending order. In present terminology, these collections would be from the upper Atrasado Formation. All are in gray to buff siltstones. A fourth, collected in 1941 and described as "base of the Red Magdalena," appears to be from near the Pennsylvanian–Permian boundary, what currently would be called the Bursum Formation. The fossils are preserved in brown to red and yellow mottled siltstones. The final set of collections comes from the Abo Formation, which is of early Permian age, corresponding to the Wolfcampian and early Leonardian in American usage (Sakamarian through early Kungurian). The Abo plants are preserved in well-cemented, light-red to deep-red siltstones and sandstones.

In terms of depositional environments, collections from below the Abo Formation are mostly from quiet-water settings, in which the plants appear to have been carried in from the surrounding landscape and to have settled to the bottom under low-energy conditions. Muscovite concentrations and comminuted plant debris drape many bedding surfaces, which is also indicative of episodic low-energy conditions with little water movement. In most of the collections, the organic matter appears to have been deposited episodically, given the significant number of surfaces that do not contain plant fossils or any sort of comminuted plant debris, suggesting that the collections were made from one or several discrete layers, around which the siltstones were barren. Three of the five collections, Units 10 and 8 and base of Red Magdalena, all from the middle of the sequence, also contain various numbers of invertebrate animal remains, principally microconchids/spirorbids, small snails, ostracods, and occasional conchostracans. A single linguloid occurrence was noted. The animals associated with these three collections suggest proximity to marine conditions and possible deposition of the plant material in water of brackish salinities (although that does not indicate that the living plants were growing in saline water). Unit 35, at the base of the sequence, and the Abo

Formation, at the top, are devoid of any animal fossils (although a terrestrial fauna is known from the Abo Formation as macrofossils and trace fossils from numerous sites throughout New Mexico).

The floras all appear to be derived from vegetation that grew under some degree of climatic seasonality. In general, the extremity of this seasonality appears to increase through the section from the oldest to the youngest assemblage. However, it must be kept in mind that, on the basis of the character of the enclosing sediments, these floras appear to have been buried and preserved under subtly to significantly different depositional conditions. Such differences also may be correlative with different degrees of landscape microhabitat heterogeneity, elevational variability, and vegetational zonation around the site of deposition of organic matter.

The oldest assemblage contains the highest concentration, based on quantitative compositional assessments, of wetland plants, such as pteridosperms, calamitaleans, sphenophylls, groundcover ferns, and marattialean tree ferns. However, plants generally considered to be typical of seasonally dry settings, such as conifers, *Sphenopteris germanica*, and some pteridosperms (mixoneurids), also are abundant in this flora. We argue that the climatic setting of this assemblage was mostly likely seasonally dry but to the least extent of all the assemblages reported herein. The other siltstone assemblages, those with indicators of nearby marine or brackish water bodies, are dominated by taxa typical of seasonally dry settings, primarily conifers of several types but also *Sphenopteris germanica* and two mixoneurid species, *Odontopteris* (*Mixoneura*) *schlotheimii* and *Odontopteris* (*Mixoneura*) *subcrenulata*. Small numbers of such plants as *Charliea*, *Taeniopteris*, and various callipterids (mainly *Rhachiphyllum*), also typical of dryland settings, characterize these intermediate floras. However, all three of these also contain wetland elements, most commonly calamitalean stems and foliage (most often *Annularia spicata*) and small amounts of marattialean fern foliage, most likely indicating that wet patches remained on the landscape—these plants are widespread through the early Permian in western equatorial Pangea and appear to have been able to locate and grow in even small areas of wet ground, as long as regional rainfall was sufficient to keep such habitats among the landscape mixture. The youngest floras, from the Abo Formation, are typically dominated by either walchian conifers or the peltaspermous seed fern *Supaia*. The Abo Canyon floras are *Supaia*-dominated for the most part, although conifers are among the floral elements; in effect, these floras are more or less identical to those found in the Abo elsewhere in the state. The only unique feature is the presence of *Sphenophyllum gilmorei*, described from the lower Permian of the Supai Formation in the Grand Canyon, which we have not found elsewhere in the Abo, nor are we aware of reports of it.

In summary, the Abo Pass floras are of significance because they record vegetational changes through the Pennsylvanian–Permian transition in the western equatorial reaches of the Pangean supercontinent. This area had been much drier for much longer than the central parts of the continent at low latitudes; the last western

Pangean coals, which are ash rich, were in the earlier parts of the Middle Pennsylvanian, whereas peat and coal formation continued through the Pennsylvanian and into the Permian in west central Pangea and into the Permian in Cathaysia, along the margin of the Tethys Ocean. Consequently, the study samples are an ecological record of the same progressive global climatic changes that were occurring across the much better known and more intensively studied central Pangean equatorial regions during this time period. However, the western floras lived within a background climatic context that was significantly different from that usually depicted for the change from the Pennsylvanian to the Permian in the more humid parts of central Pangea. Nonetheless, as noted by many authors (e.g., Gillespie and Pfefferkorn, 1979; Pfefferkorn and Gillespie, 1980; Blake et al., 2002; Bashforth et al., 2016), most of the same species known from central Pangea can be found in these western settings, bespeaking large biogeographic ranges and pointing to migratory pathways or other means (e.g., long-distance dispersal) of maintaining species continuity across these vast areas.

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Walchia piniformis, 4, 14
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