PENNSYLVANIAN-PERMIAN VEGETATIONAL CHANGES IN TROPICAL EURAMERICA

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INTRODUCTION

Vegetational changes across the Pennsylvanian-Permian boundary are recorded in several largely terrestrial basins across the Euramerican portions of equatorial Pangea. For the purposes of this paper, these include the Bursum-Abo Formation transition and its equivalents in several small basins in New Mexico, the Halgaito Formation of southeastern Utah, Markley Formation of the eastern shelf of the Midland Basin in north-central Texas, Council Grove Group of northern Oklahoma and southern Kansas, and Dunkard Group of the central Appalachian Basin. This transition also is recorded in numerous basins in Europe, reviewed by Roscher and Schneider (2006), based on paleoclimate indicators preserved in those regions. Collectively, these deposits form a west-to-east transect across the Pangean paleotropics and thus provide a paleogeographic setting for examination of both temporal and spatial changes in vegetation across the Pennsylvanian-Permian boundary (Figures 1 and 2).

The Pennsylvanian-Permian transition records the change from wetland vegetation as the predominant assemblages found in the plant fossil record, to seasonally dry vegetation. This has often been called the "Paleophytic-Mesophytic" transition, a concept that is flawed

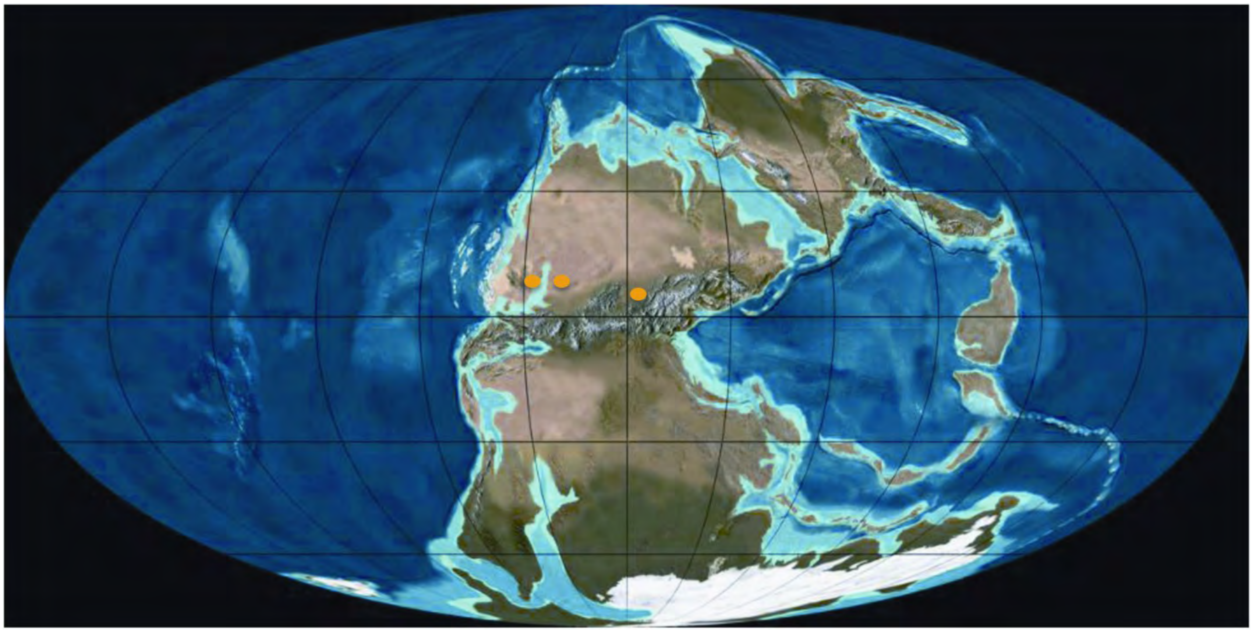

Figure 1. Continental configuration at the Pennsylvanian-Permian boundary. Yellow ovals indicate the principal areas discussed herein: Left – New Mexico and Utah, Center – Texas and Oklahoma, Right – Central Appalachians/Dunkard. Map courtesy of Ron Blakey, Northern Arizona University.

DiMichele, W. A., Cecil, C. B., Chaney, D. S., Elrich, S. D., Lucas, S. G., Lupia, R., Nelson, W. J., and Tabor, N. J., 2011, Pennsylvanian-Permian vegetational changes in tropical Euramerica, *in* Harper, J. A., ed., Geology of the Pennsylvanian-Permian in the Dunkard basin: Guidebook, 76th Annual Field Conference of Pennsylvania Geologists, Washington, PA, p. 60-102.

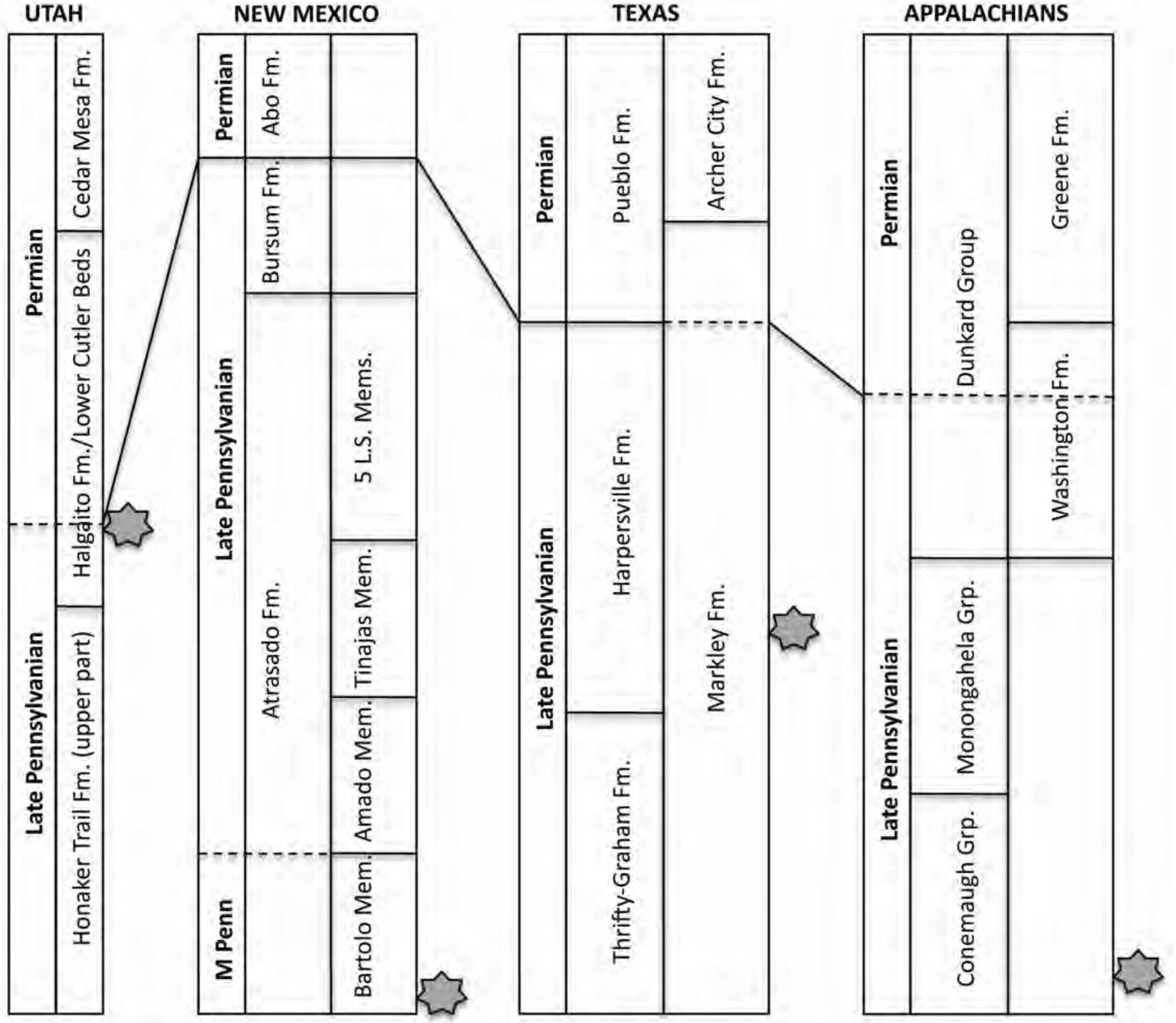

Figure 2. Stratigraphic sections for the areas discussed herein, positioned West-to-East along the Pangean paleoequator. Stars indicate the position of the first appearance of seasonally dry flora in the local stratigraphic section. Solid lines are accepted temporal boundaries or boundaries of formations or groups. Dotted lines are inferred temporal boundaries.

conceptually but does reflect a pattern of vegetational change at a certain coarse level of resolution (DiMichele et al., 2008). Interpreted simplistically, this change is asynchronous across the Pangean tropics. In detail, however, it is clear that “dry” floras appear as early as the Middle Pennsylvanian in central and western Pangea (Scott et al., 2010; Falcon-Lang et al., 2009; Plotnick et al., 2009; Galtier et al., 1992; Dolby et al., 2011), and that coals are effectively gone from the stratigraphic record of far western Pangea after the end of the Atokan (Bolsovian, mid-Moscovian) (Lucas et al., 2009a). In contrast, organic facies persist, even if much reduced in thickness, quality and abundance, together with associated wetland plants, into the Early Permian in central and east-central Pangea, at the same time as deposits dominated by plants of seasonally dry environments are increasing in frequency (e.g., Martin, 1998; Kerp and Fichter, 1985).

When the complexity of this transition is embraced, it is found that its nature takes on different qualities depending on the spatial and temporal scale at which it is resolved and examined. On the temporal scale of glacial-interglacial cycles, floras consisting of species tolerant of seasonal moisture deficits are found intercalated with floras of humid environments, resulting in the alternation of taxonomically distinctive assemblages, at least on the northern side of the Appalachian-Variscan central Pangean mountain range (Mapes and Gastaldo, 1986; Broutin et al., 1990; DiMichele and Aronson, 1992 – the history and dynamics of this mountain belt were complex, such that the mountain range was not contemporaneously present across the Pangean continent, as is frequently shown in paleogeographic reconstructions – see discussion in Roscher and Schneider, 2006). In some instances, this floristic alternation can occur between different beds of the same outcrop (DiMichele et al., 2005a; Falcon-Lang et al., 2009). The changing floras reflect climate contrasts that have been interpreted to change in concert with glacial-interglacial cyclicity (Falcon-Lang, 2004; DiMichele et al., 2010c; Falcon-Lang and DiMichele, 2010). Such vegetational cyclicity is interpreted in this paper to reflect shifts between cool-wet (glacial) and warm-dry (interglacial) (Cecil and Dulong, 2003) tropical climate states. Furthermore, the cyclicity observed for vegetation, and inferred for climate, occurs within depositional packages interpreted to result from sea-level changes, recorded in the classic Pennsylvanian cyclothems. Also seen are climate trends on longer time scales of 2-6 million years (Darrah, 1969; Cecil, 1990; Falcon-Lang et al., 2011a; Allen et al., 2011) linked to extended periods of drier climate, higher mean sea-level, and reduced polar ice volume (Fielding et al., 2008; Rygel et al., 2008; Eros et al., in press). At the longest temporal scale is the long-recognized trend toward drier tropics manifested in the Pennsylvanian-Permian transition in the western and central parts of equatorial Pangea (Remy, 1975 for discussion from a paleobotanical perspective). This longest-term trend is not monotonically unidirectional, but is an average of an oscillatory trend ultimately leading to a reduction in the number and length of intervals of significantly wet tropical climate. Within this longer-term trend it might be said that climate fluctuations continue, but that, on average, the wet periods become less wet and the dry periods become more dry. Cecil et al. (2011) suggest that this trend is due either to the final assembly of Pangea or to the rise of the central Pangean mountains. The trend happens, inexplicably, at a time when evidence has been adduced for the return of large amounts of ice at the beginning of the Permian (e.g., Montañez et al., 2007; Fielding et al., 2008).

BASES OF INFERENCE/RATIONALE

The environmental preferences of fossil plants can be resolved in many environmental dimensions. Very commonly, however such preferences are broadly construed as favoring habitats with year-round high soil-moisture content or environments where there are seasonal deficits of moisture. These preferences are determined from plant architecture, growth habit, and environmental correlates of occurrence, including the sedimentary environments in which the fossils are found. Such inferences come from the literature and from the personal experiences of the authors, which are both published and unpublished. The extent to which such patterns are reflective of regional climates is contextual, dependent on broader spatial and temporal patterns of floristic occurrence, the sedimentological context of the floras, and the extent of the depositional systems of which they are a part. Consequently, the focus herein is more on the plants and less on the accessory information that accompanies the paleobotanical samples. That said, there are clear preservational biases in the fossil record of plants. Paleosols tell us that vegetation was present during the times of drier climate, but we have a limited understanding of that vegetation, at least at present, despite a considerable number of publications that discuss it (for recently published papers see, for example, Feldman et al., 2005; Falcon-Lang et al., 2009; Plotnick et al., 2009; Scott et al., 2010; DiMichele et al., 2010c; Falcon-Lang et al., 2011a; Dolby et al., 2011). The dry soil plants do become well represented in the Permian fossil record of the equatorial region, reflecting, perhaps, changed sedimentary systems and changed paleobotanical search images (Kerp, 1996).

To the extent possible, we consider information from paleosols relevant to rainfall and water table, sedimentary patterns, geochemical proxies for various aspects of climate, climate modeling, near-field studies of the ice record, and other sources of information (e.g., Cecil et al., 2003; Feldman et al., 2005; Montañez et al., 2007; Tabor and Montañez, 2004; Poulsen et al., 2007; Tabor and Poulsen, 2008; Tabor et al., 2002, 2008; DiMichele et al., 2010c; Horton et al., 2010).

In a glacial world, there also is very likely to be a close, mechanistic relationship among tropical climate, sediment transport patterns, global sea-level dynamics, polar ice-volume, and the composition of the atmosphere. This is framed broadly, though not entirely, by considering rock stratigraphic sequences in terms of a combined climate-sea level-tectonics framework (Cecil and Dulong, 2003; Poulsen et al., 2007; Elrick and Nelson, 2010; Allen et al., 2011; Eros et al., in press). Here we are operating under the presumption that sea-level lowstand, particularly from its midpoint into the earliest phases of sea-level rise, is associated with the wettest equatorial climates. If peats/coals are present in a cycle, this is the most likely time for them to have formed. The driest equatorial climates occur at sea-level highstand and continue, diminishing, into the phases of sea-level fall.

It is during these stages of the cycle that limestones, evaporites, and paleosols indicative of seasonal climates are most likely to form. This model (Cecil et al., 2003; Poulsen et al., 2007; Eros et al., in press) has been slow to emerge for several reasons. Perhaps foremost is incumbency. Earlier models, such as that of Bohacs and Suter (1997), which call upon sea-level rise to initiate and sustain cratonic-basin blanket-peat formation, treat climate as a constant (e.g., p. 1618, where they note that “only accommodation varies significantly and most other variables remain constant (flora, climate, environment, etc.)”). This, in effect, removes climate as a variable in their sequence stratigraphic model, without specifying the state of that invariant climate. Such models, therefore, attribute all changes in lithological sequences to sea-level changes. When considered within a “total evidence” framework, however, these models fall short. For example, were sea-level rise the driver of peat formation, it is then necessary to explain why, during the late Paleozoic, peat beds did not form in the western parts of the Pangean equatorial region while, at the same time, extensive peats were forming in the Midcontinent and eastern coal basins (e.g., Cecil et al., 2003; Bishop et al., 2010). Furthermore, modern sea-level rise has not created vast peat-forming swamplands along coastlines worldwide.

The prevailing understanding that the modern tropics are wettest during interglacials and dry during glacial phases of glacial-interglacial cycles is not as much an iron-clad truth as assumed, and is changing as greater study of historical Amazonian climate patterns emerges. The Amazonian lake record is consistent with an equatorial band of the Amazon being wettest at or near glacial maximum, possibly caused by constraint of the intertropical convergence zone (ITCZ) (e.g., Bush et al., 2002). In addition, the great majority of modern Amazonian interglacial rainfall reflects recycling of water by the tropical rainforest (e.g., Bush and Flenley, 2007), something that may be entirely dependent on the presence of angiosperms and their unique water transport and evapotranspirative capacities (Boyce and Lee, 2010; Boyce et al., 2010). The latter point means that pre-angiospermous systems, such as those of the late Paleozoic, may not have been able to create "rainforest" levels of moisture over large areas during inter-glacial episodes (Remy, 1975). Without the powerhouse evapo-transpiration created by the angiosperms, the implication is that tropical wetness must have been generated by a largely physical mechanism (e.g., the restriction of the ITCZ by polar ice and attendant atmospheric conditions at the ice front – Cecil et al., 2003).

SPATIAL PATTERNS WITHIN THE PALEOEQUATORIAL REGION

The main geomorphological trend that is most easily observed and tracked in space and time is the presence or absence, or relative abundance, of coal and the subjacent "underclay" paleosols (Cecil et al, 2003; Cecil et al., 2011). Well developed "underclay" paleosols can often be traced in somewhat elevated areas well beyond the occurrence of the superjacent coal beds where soils with aquic to udic soil moisture regimes inhibited or even excluded the development of peraquic conditions that are conducive to the development of histosols (peat precursors to coal) on the land surface (Cecil et al., 2011). The physical, chemical, and mineralogical properties of the underclay paleosols beneath coal beds clearly indicate low stand sea level conditions and pedogenesis under a humid to perhumid paleoclimate. Thus, coal represents the "wettest" (glacial) climate phase of a glacial-interglacial cycle when rainfall was sufficient to perpetually maintain the water table at the surface.

Also relatively readily observed as indicators of climate are seasonally-dry floral elements. It is possible to assess: (a) their "on-average" abundance or the commonness with which they are encountered in a particular geological unit, such as a formation, (b) their degree of mixing with the more hygromorphic (wetland) floral elements, and (c) the time, or times, at which they first appear and/or become the most commonly encountered vegetational elements. With regard to this latter point, "dominance" is a term we will use with caution and constrain to relative abundance within a single fossil assemblage, which is considered herein a proxy for a natural plant community. The term "dominance" when expanded to larger temporal or spatial scales implies the existence of a single vegetation type or species pool in equilibrium with, or responding to, a monotonic climate. Rather, we see two or more distinctive, climatically characteristic species pools reflective of different mean climate states (sensu Cecil et al., 2011). The presence of these different species pools in sedimentary basins is a response to changes in soil moisture. Soil moisture changes, allowing for the ever-present effects of local edaphics, may reflect changes in regional climate brought about by glacial-interglacial cyclicity. As mentioned previously, we consider climatic cyclicity within a single glacial-interglacial cycle to be wet/cool during sea level lowstands (maximum ice volume) and seasonally dry during sea level highstands (minimum ice volume). These glacial-interglacial patterns, on the 10^5-year time scale, will be superimposed on the longer term changes in climate, on the 10^6, 2 to 6 million year scale (Allen et al., 2011), when mean climate state was overall warmer-drier or cooler-wetter, reflective of changes in mean global ice volume and sea-level. And patterns on both these time scales will be encapsulated within the long term Pennsylvanian-Permian climate change, on the 10^7-year time scale.

At the 10^7-year, Pennsylvanian-Permian time scale, there clearly is a trend toward overall drier climate beginning in the late Middle Pennsylvanian and continuing through the Early Permian (Remy, 1975; Roscher and Schneider, 2006; Tabor and Poulsen, 2008), perhaps attributable to the final assembly of the mega-continent Pangea, the northward drift of the continental landmass, and changes in atmospheric and oceanic circulation (Cecil, 1990; Parrish, 1993; Roscher and Schneider, 2006; Tabor et al., 2008). During glacial-interglacial oscillations, this means that the wetter phases became less wet and the drier phases became even drier. This pattern, ultimately, permits the survival in basinal lowlands of plants more tolerant of moisture seasonality, at all phases of the cycle. As basinal landscapes “dry out” over time, the wetland specialist plants become less common and often are spatially concentrated, occurring together as habitat specialists in reduced diversity assemblages in landscape “wet spots” (DiMichele et al., 2006).

Westernmost Pangea: New Mexico and Southeastern Utah

During the late Paleozoic, present day New Mexico was located in the western part of equatorial Pangea as an archipelago of basement cored uplifts surrounded by shallow marine and, in some cases, locally terrestrial basin floors of the Ancestral Rocky Mountain basin and range (Figure 1). This region of the supercontinent appears to have been persistently more seasonally dry than more central parts of the megacontinent throughout the later Pennsylvanian and into the Early Permian, with a distinct monsoonal pattern of precipitation, evidently sourced from Panthalassa rather than Tethys (Parrish, 1993; Tabor and Montañez, 2004; Tabor and Poulsen, 2008). Glacial-interglacial scale lithological cyclicity is more obscure in this region than in the central Pangean coal basins due in large part to the near absence of coal/underclay as a low-stand marker bed. Cyclicity can be detected in some of the marine (Elrick and Scott, 2010) and terrestrial Pennsylvanian sections, and in mixed marine and terrestrial Lower Permian rocks (Mack et al., 2010). It also can be detected as the higher-level, stage-scale fluctuations in climate state (sensu Cecil et al., 2011), e.g., a much drier Missourian (Kasimovian) than either the earlier Desmoinesian (Moscovian) or the later Virgilian (Falcon-Lang et al., 2011a), and in the same overall drying trend that characterizes the Pennsylvanian-Permian transition in general (Remy, 1975; Cecil et al., 1985; Cecil, 1990).

Our studies in New Mexico reveal the shift from wetter-to-drier climates earlier than any other area we have examined in detail. In the central part of the state, Socorro County, a nearly complete lithological transition, with associated flora and both marine and terrestrial fauna is preserved from the Middle Pennsylvanian to the Early Permian (Lucas et al., 2009a; Krainer and Lucas, 2009). The Pennsylvanian-Permian transition is well exposed in both this central region, and to the north in areas near Albuquerque (Lucas and Krainer, 2004; Krainer and Lucas, 2004; Lucas and Zeigler, 2004), and still farther north in areas to the west of Sierra Nacimiento, east of Cuba (Lucas et al., 2010a, b; Krainer and Lucas, 2010; DiMichele et al., 2010a). Seasonally-dry floral elements begin to appear in the Middle to Late Pennsylvanian in each of these areas (depending on the age of the oldest exposed terrestrial rocks) and are a part of nearly every plant assemblage collected thereafter, becoming outright the overwhelmingly most common vegetation type either in the later part of the Late Pennsylvanian, in the Bursum Formation or in the wholly Lower Permian Abo Formation (e.g., Mamay and Mapes, 1992; Utting et al., 2004; Tidwell and Ash, 2004; DiMichele et al., 2004; DiMichele et al., 2007; Lucas et al., in press a). Geological ages throughout New Mexico are among the best constrained of any of the Pennsylvanian-Permian transition regions considered in this paper, all accurately calibrated with conodonts and/or fusulinids from adjacent and intercalated marine strata (e.g., Lucas et al., 2009a).

Floras from these areas require some explanation because of their mode of preservation. In the Atokan (Bolsovian/middle Moscovian) Sandia Formation, coal beds are represented only by a few isolated lenses, geographically very localized (e.g., Thompson, 1942; Armstrong et al., 1979; Kues and Giles, 2004; Krainer et al., 2011) and not thick enough or laterally extensive enough to be of economic significance. They are associated with wetland floras (Lucas et al., 2009b), but are not even remotely comparable in extent to coal-forming paleoenvironments of similar age in the eastern USA and in Western Europe. Paleosol deposits, so called “fire clays”, associated with the coal beds have been mined locally for brick and pottery (Lucas et al., 2009b), and indicate periods of humid to perhumid climates and intense weathering.

The Desmoinesian (Asturian/late Moscovian) in New Mexico reflects a time of elevated sea levels relative to the earlier Pennsylvanian, as across much of the Ancestral Rocky Mountain zone, with local tectonics creating an essentially non-marine basin floor setting in an area east of Socorro, central New Mexico, that persisted through the late Missourian (Lucas et al., 2009a). In this area, glacial-interglacial-scale oscillation of wetland and seasonally-dry floras can be detected in parts of the section. The wetland floras, although rare, are authochthonous to parautochthonous and completely dominated by typically Pennsylvanian wetland plants, such as pteridosperms and *Psaronius* tree ferns. These assemblages appear to be preserved in lowstand coastal-plain deposits, based on their sequence position (lowstand), and sedimentary characteristics (thin, widespread, autochthonous, rooted siltstone deposits). They are intercalated with shales that appear to represent marine high-stand to falling-stage shallow shelf deposits, containing brackish-to-marine fauna and allochthonous plant remains (Figure 3). These latter floras contrast sharply with those of the lowstand, wetter phases, and contain predominantly the xeromorphic/seasonally dry plants, such as *Sphenopteris germanica*, *Charliea*, and walchian conifers, with admixtures of wetland elements, mainly pteridosperms (DiMichele et al., 2010b). The Missourian of this area is particularly dry (Lerner et al. 2009; Falcon-Lang et al, 2011a) (Figure 4), as it appears to be across the North American part of the Pangean tropics (Cecil et al., 1985; Cecil, 1990; Martino and Blake, 2001; Martino, 2004; DiMichele et al., 2010b; Cecil et al., 2011). Floras preserved in Socorro County vary from completely dominated by seasonally-dry substrate species, including conifers, callipterids, *Charliea*, *Taeniopteris* and *Sphenopteris germanica* (Falcon-Lang et al., 2011a), to mixed, with wetland elements forming a background to primarily seasonally-dry substrate taxa (Lerner et al., 2009). A coeval flora of Missourian age is known from 100 km (62 mi) to the north, near Albuquerque, from the Kinney Brick Company quarry in the Manzanita Mountains (Mamay and Mapes, 1992). This deposit was formerly thought to be of middle Virgilian age, is dominated by wetland plants, but has a well represented and diverse array of seasonally dry-substrate taxa, including *Sphenopteris germanica* (*Sphenopteridium manzanitanum*, Mamay, 1992), *Charliea manzanitana* (Mamay, 1990), *Dicranophyllum readii* (Mamay, 1981), several forms of conifer and pteridosperms typically found in drier substrate settings (Lucas et al., in press a).

At the Pennsylvanian-Permian transition, including the Bursum (and its equivalents) and lower Abo formations (Lucas and Krainer, 2004; Krainer et al., 2009; Krainer and Lucas, 2010; Mack et al., 2010), floras are regionally variable and show different mixtures of wetland and seasonally dry elements. In Socorro County, Bursum floras are preserved in coastal plain environments (Figure 5A) that are not substantially different from those of the Desmoinesian and Missourian in the same area. These floras are, however, dominated by dryland species,

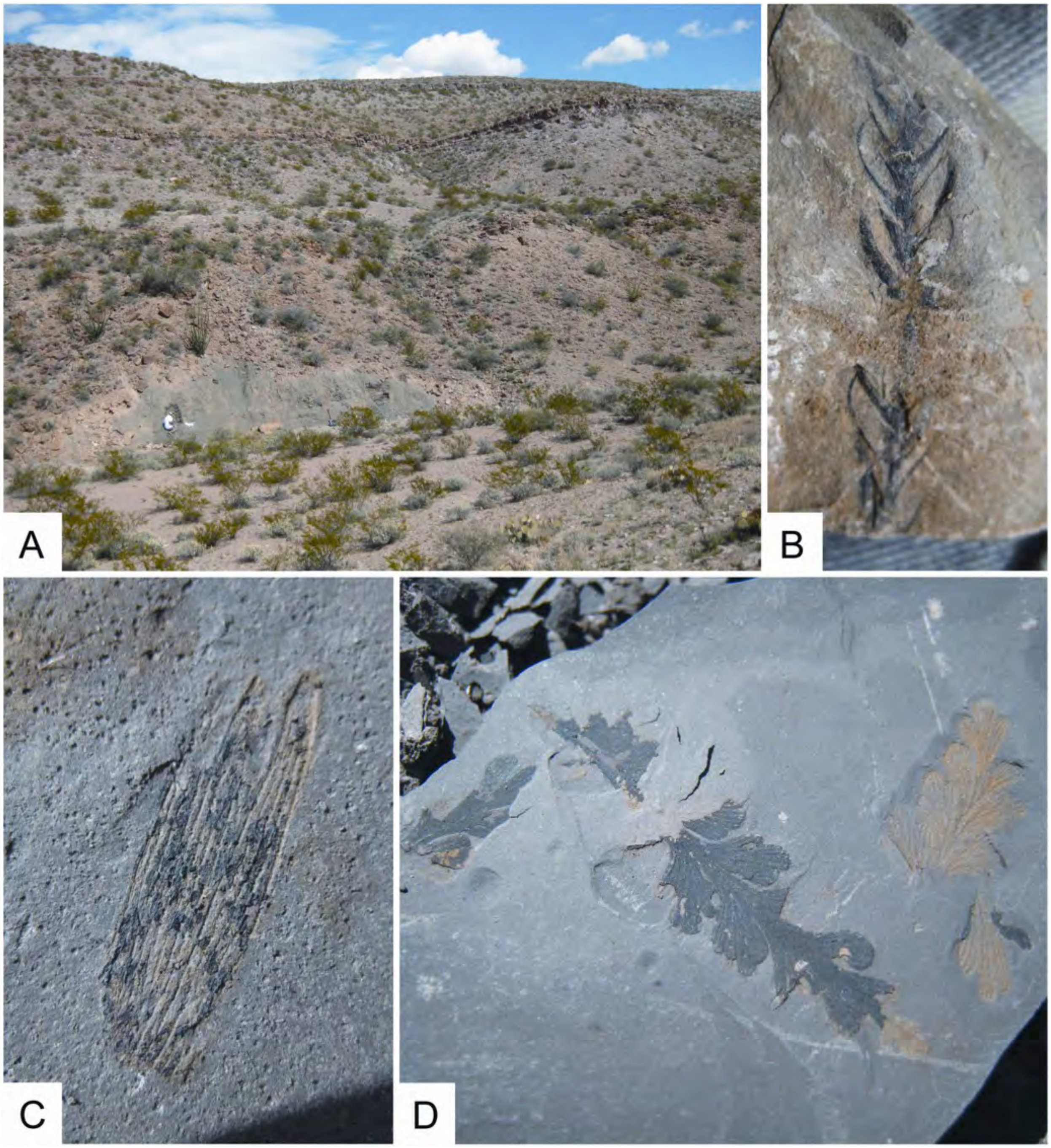

Figure 3. Desmoinesian (Middle Pennsylvanian) age exposure and plants from the Bartolo and Tinajas members of the Atrasado Formation, Socorro County, New Mexico. A—Bartolo Member – two lower shales separated by calcareous sandstone, each contain allochthonous, seasonally dry flora. Crest of ridge marks the position of the Amado Member, immediately above the Desmoinesian-Missourian boundary. B—Walchian conifer twig with leaves (USNM 543964; USNM loc 43527). C—*Charliea* pinnule (USNM 543967; USNM loc 43469). D—*Sphenopteris germanica* pinnae (USNM 508828; USNM loc 43469). All specimens approximately 3 X magnification.

including walchian conifers and cordaitaleans. The similar sedimentary environments permit an isotaphonomic comparison (sensu Behrensmeyer and Hook, 1992) and suggest that the wettest intervals of climate cycles were significantly drier than during earlier time periods in the Desmoinesian through Virgilian. In the Lucero Uplift, 80 km (50 mi) to the NNW of the

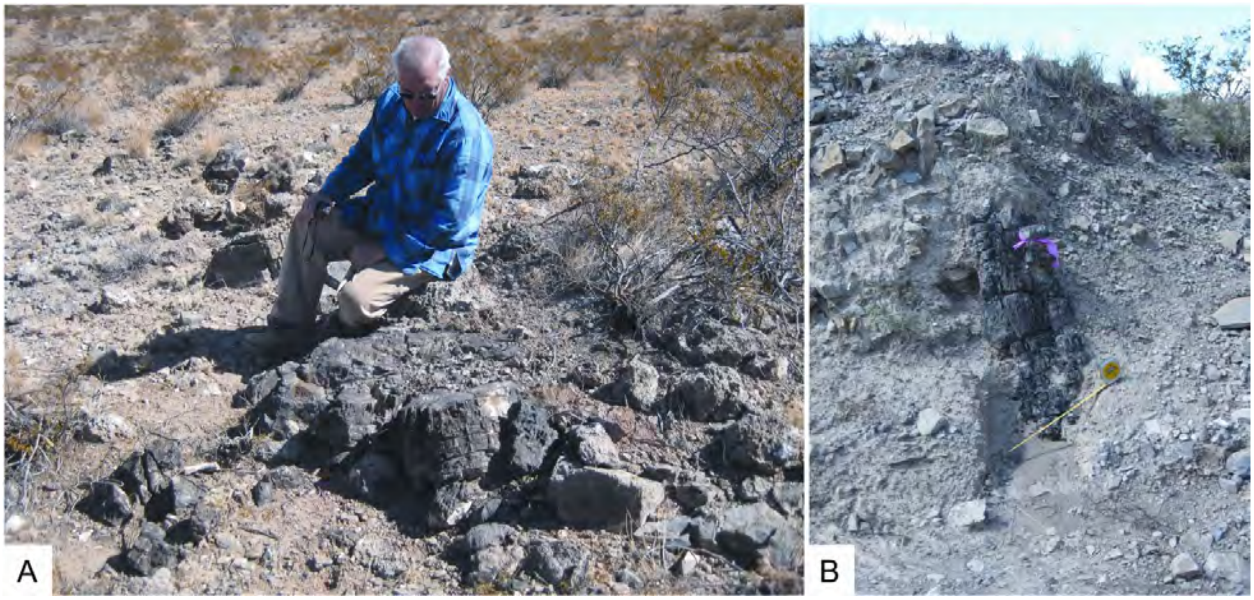

Figure 4. Missourian (Late Pennsylvanian) gypsum-carbonate sabkha deposit, Tinajas Member of the Atrasado Formation, Socorro County, New Mexico. The bases of coniferopsid (conifers or cordaitaleans) trees are preserved within this deposit, rooted in micritic limestone and buried by gypsum and carbonate (see Falcon-Lang et al, 2011a). A—Large tree base with attached roots, extending into the basal micrite, exposed by erosion of the gypsum-carbonate bed. B—Tree trunk extending upward into the gypsum-carbonate bed (scale = 50 cm).

Socorro area, latest Pennsylvanian floras from the Red Tanks Member of the Bursum Formation are also preserved in lacustrine sediments within a coastal plain setting. Conditions were rarely humid enough to engender peat/coal formation (Krainer and Lucas, 2004). The plants are predominantly wetland taxa but with a large admixture of conifers, callipterids and taeniopterids (Carrizo Arroyo flora, see Tidwell and Ash, 2004), all elements of seasonally dry vegetation. Such a mixed flora suggests that the wetland species were confined to wet places on an otherwise seasonally dry landscape (as suggested for the regional climate by Krainer and Lucas, 2004). The northern-most Late Pennsylvanian plant-bearing strata (El Cobre Canyon Formation, a Bursum equivalent, and Lower Permian Arroyo del Agua Formation) (Lucas et al., 2010b), were deposited in braided river systems (Krainer and Lucas, 2010). The floras are numerically dominated by wetland plants, like those from the approximately equivalent aged Red Tanks Member in the Lucero Uplift, but, as there, these wetland elements appear to have been drawn from stream banks or from locally colonized areas within the shifting braidplains. Most of the assemblages contain uncommon, but consistently present, plants from substrates that were likely seasonally dry, such as walchian conifers, *Taeniopteris* and cordaitaleans (DiMichele et al., 2010a).

In all regions of New Mexico, the Early Permian rocks record the long-term transition to a seasonally drier climate mean at all stages of climate cycles (Mack et al., 1991; Krainer and Lucas, 2010). Depending on facies, the flora of these Early Permian rocks varies considerably. A major facies change takes place as a consequence of a pulse of the Ancestral Rocky Mountain uplift beginning in the early Wolfcampian (latest Pennsylvanian). This produces the synorogenic Abo Formation, which formed on a vast coastal plain, represented by channel-form fluvial deposits and overbank siltstones and mudstones (Figures 5B, 6). Abo Formation exposures are intercalated with marine deposits of the Hueco Group in southern New Mexico,

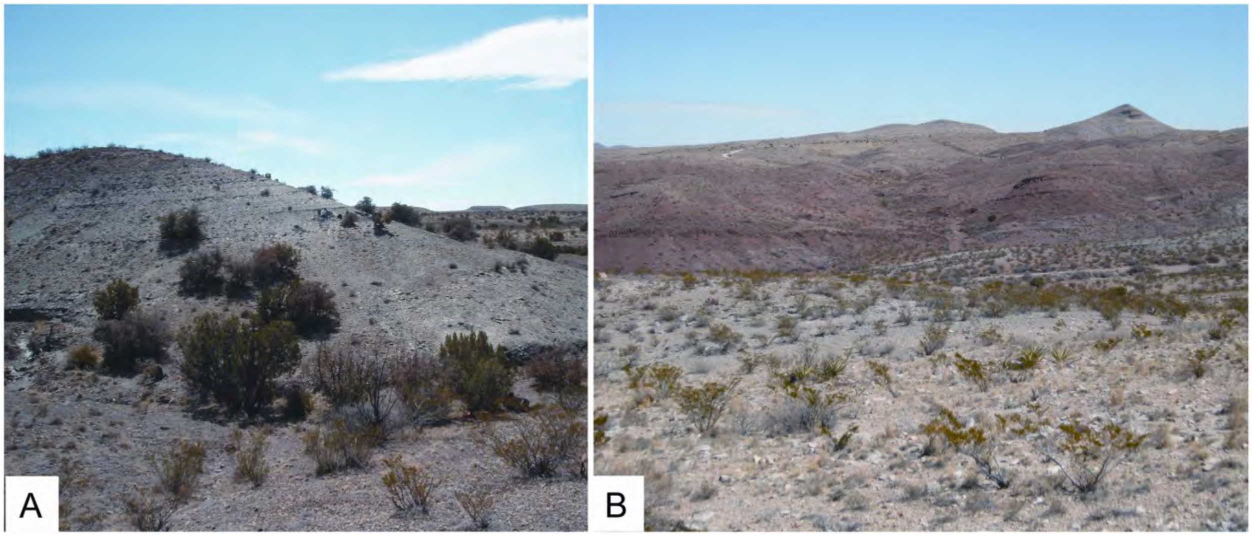

Figure 5. Wolfcampian (latest Pennsylvanian) age Bursum Formation and Early Permian age Abo Formation, Socorro County, New Mexico. A—Bursum Formation plant-bearing shales, perhaps deposited in a floodplain lake. Most of the Bursum consists of paleosols and limestones, and is without plant fossils. B—Succession in the Socorro County area: Atrasado Formation (white, limestone in foreground), Bursum Formation (gray, low slope and hills in middle foreground), Abo Formation (red hills), Yeso Formation (yellow-gray hills on skyline). Pennsylvanian-Permian boundary lies at the Bursum-Abo contact just above the center of the photograph.

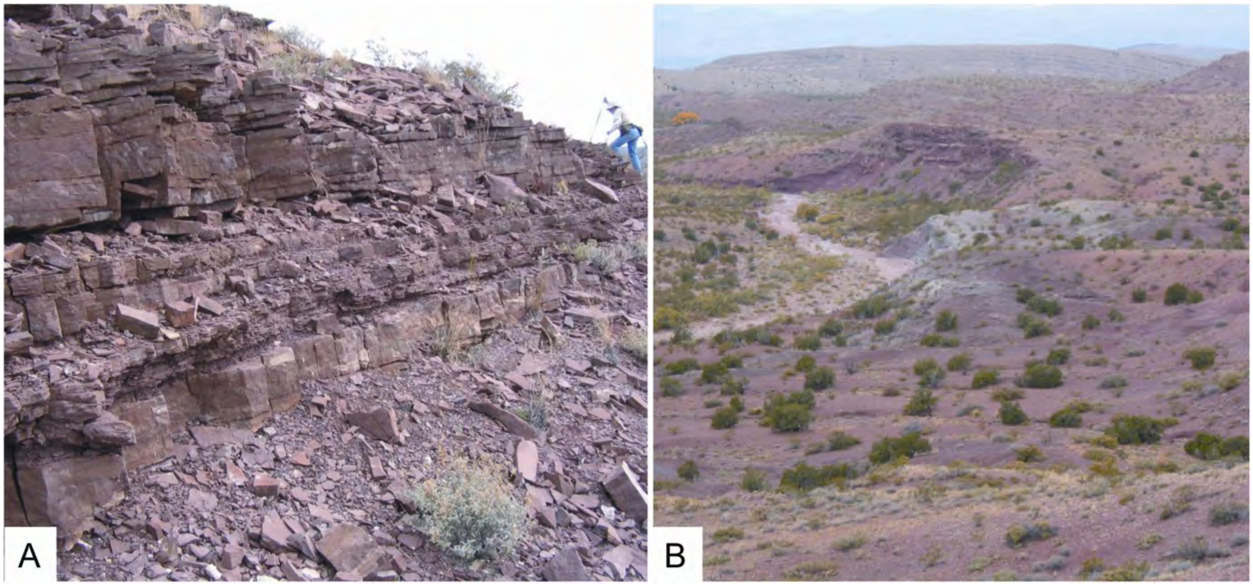

Figure 6. Early Permian age Abo Formation, Socorro County, New Mexico. A—Siltstone channel fill characteristic of deposits in which plants are commonly found. B—Lower and Middle portions of the Abo formation shown in stream cutbank. Siltstones with strong pedogenic overprint characterize the lower portions of the Abo Formation. Thin, sheet siltstones and fine grained sandstones are generally more common in the middle and upper part of the Abo Formation.

(Lucas et al., 1995), but otherwise the Abo is entirely terrestrial, with thick calcic Vertisols and stream deposits, with loessites further to the north (Mack et al., 1991; Kessler et al., 2001; Mack et al., 2003; Mack, 2007). The flora from these beds comes primarily from siltstones of the channel facies and is of remarkably low diversity (DiMichele et al., 2007), consisting of patches of various walchian conifers and the peltasperm *Supaia*, with a small, and generally rare,

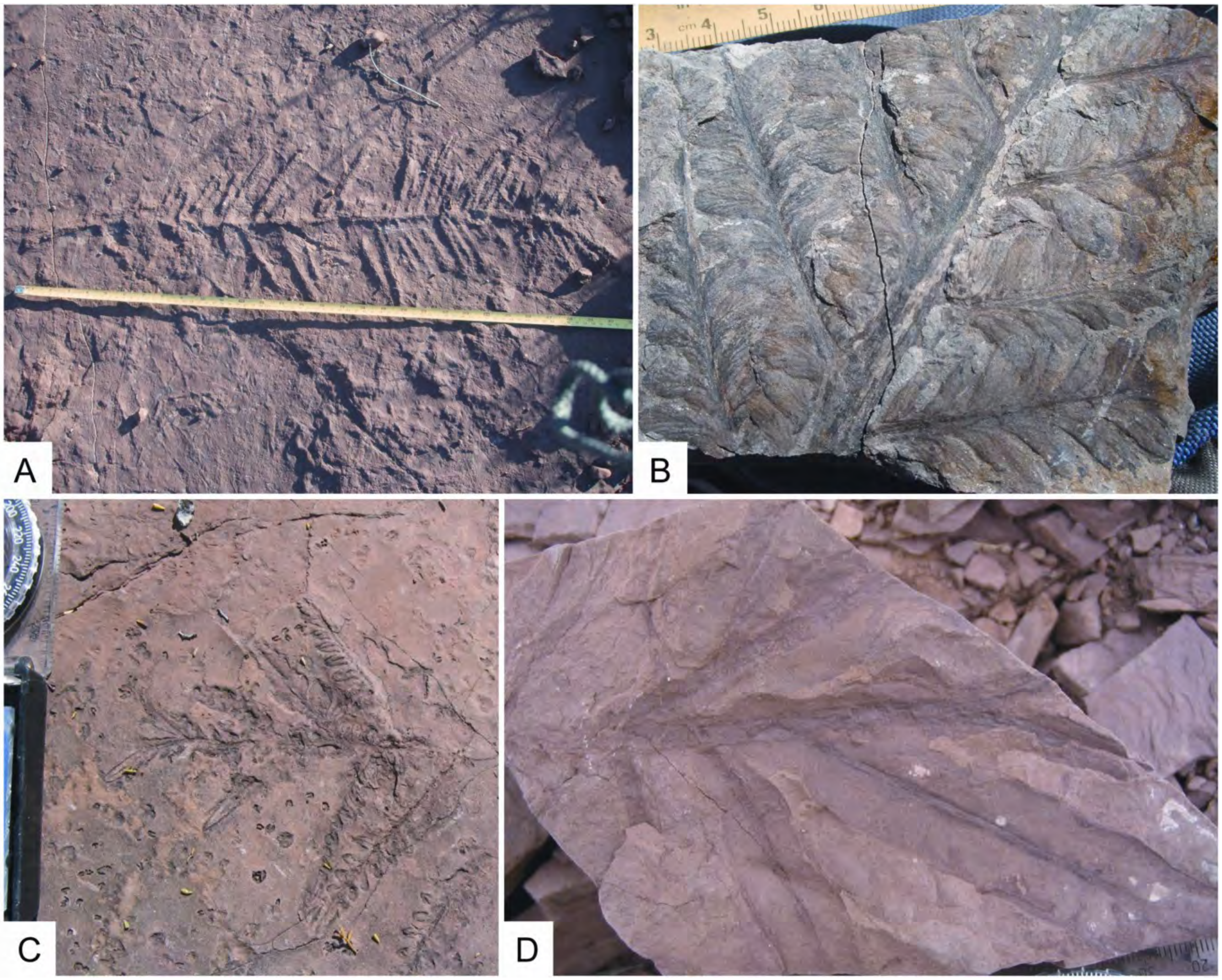

Figure 7. Plant fossils typical of seasonally dry flora, from the Bursum and Abo formations, Socorro County, New Mexico. A—Walchian conifer branch (field photo; specimen not collected). B—*Rhachiphyllum* sp., callipterid peltasperm frond segment (USNM 543963; USNM loc. 43460). C—*Autunia conferta*, callipterid peltasperm frond segment (tip) (USNM 543955; USNM loc. 42251). D—*Supaia anomala*, supaioid peltasperm leaf fragment (USNM 543956; USNM loc 42255).

admixture of callipterids and other plants of seasonally dry habitats (Figure 7). This is particularly true for the central and southern areas of the state. In the northern areas, such as Arroyo del Agua, the flora is more diverse than in the typical Abo redbeds, but of lower diversity than the Late Pennsylvanian floras of the same area. The most common elements include conifers, callipterid peltasperms, and *Taeniopteris*, all seasonally dry plants. However, there also are the common wetland elements, calamitaleans, pteridosperms, and tree ferns, that probably grew within the floodplains of braided stream systems (DiMichele and Chaney, 2005).

Approximately 500 km (311 mi) to the NW of Socorro County, and perhaps at the margin of the paleotropical, equatorial belt (Dubiel et al., 1996), are deposits at the Pennsylvanian-Permian boundary in southeastern Utah (Figure 8). The sedimentary systems in this region reflect greater aridity at all times than those in New Mexico (Soreghan et al., 2002; Tabor et al., 2008), with regional climate varying from arid (aeolian dune sands, loessites and Calsisols) to subhumid (rivers and flood plains with Calcisols, colonized by plants). Keeping in mind that this area is paleolatitudinally north of the equatorial region, there appears to be an overall trend

Figure 8. Setting Hen Butte, Valley of the Gods, southeastern Utah. Stratigraphic succession. Camera angle causes the apparent overlap in the units. Late Pennsylvanian Honaker Trail Formation. Pennsylvanian-Permian Halgaito Formation. Early Permian Cedar Mesa Formation.

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from semiarid during the early Late Pennsylvanian to seasonally wetter conditions in the Early Permian (Soreghan et al., 2002). Like the Abo Formation, in New Mexico, the Early Permian deposits in southeastern Utah are significantly more "inland" than older rocks of the Late Pennsylvanian.

In a simplified stratigraphy from this area, the Middle and Late Pennsylvanian strata are assigned mostly to the Honaker Trail Formation, the uppermost part of which is represented by a cyclic series of paleosols, channel or braidplain sandstones, non-marine limestones and shales possibly reflective of a strong global-scale, allocyclic eustatic signal (Hite and Buckner, 1981; Soreghan et al., 2002). We did not find any plant macrofossils, other than a few unidentifiable axes, in these latest Pennsylvanian rocks, though a flora composed entirely of Pennsylvanian wetland species was reported from clastic rocks in the Honaker Trail Formation, 150 km (93 mi) to the north, near Moab, Utah (Tidwell, 1988). Palynological analyses of clastic and evaporitic rocks from the Paradox Formation of SE Utah, which is of Desmoinesian age (Middle Pennsylvanian), were carried out by Rueger (1996). Substantial climate cycling at this time is detectable from these analyses, as it was in similar age rocks from New Mexico. Overall, the SE Utah palynological assemblages are dominated, on a percent-abundance basis, by striate bisaccate monosaccate grains, generally considered suggestive of seasonally dry flora. However, these grains cycled in abundance through halites and their clastic interbeds. Typical wetland-flora palynomorphs were found to be rare but present (including *Lycospora*), and were negatively correlated with striate bisaccate grains.

The Honaker Trail Formation is overlain by the Halgaito Formation, which in the Valley of the Gods, in SE Utah (~ 16 km [~10 mi] north of Mexican Hat, Utah), consists of eolian sandstones and loessites, non-marine limestones, paleosols indicative of seasonally dry climates, and water-lain sandstones of various geometries, from thin bedded and flat-bottomed to bar forms of moderately large channels (Soreghan et al., 2002; Tabor et al., 2008). The Halgaito is thought to cross the Pennsylvanian-Permian boundary (e.g., Condon, 1997), and contains well preserved plant fossils. It is overlain by eolian sands and evaporites of the Cedar Mesa Formation (Loope, 1984, 1985, 1988).

The Halgaito Formation in the Valley of the Gods and Monument Valley contains both plants and non-marine aquatic and terrestrial vertebrate fossils. The vertebrates are found mainly in carbonate facies and conglomeratic deposits in small channels (Vaughn, 1962; Scott and Sumida, 2004), and are represented by taxa typically found in the Early Permian from elsewhere in the southwestern and eastern United States. Plants have been known from this region for many years (Vaughn, 1962, 1973; Mamay and Breed, 1970), though no thorough paleobotanical study of them has been undertaken. Specifically, in the Valley of the Gods, these plants are confined, for the most part, to various facies of a widely traceable interval consisting of channel cut-and-fill features. The flora was predominantly calamitalean sphenopsids and tree ferns, mainly preserved as trunks of relatively large size (10-15 cm [4-6 in] in diameter) that had been only locally transported. As with deposits of similar age in New Mexico, the flora also contained a background of plants typical of seasonally dry substrate environments, including walchian conifers. This, again, leads us to conclude that the preservation of parautochthonous, well preserved, typically wetland plants within channel facies strongly suggests a riparian flora growing along and perhaps within these channels where soil moisture was high for much of the year. However, the background of drier-site plants suggests that the landscape outside of the riparian zone was populated by plants tolerant of seasonal drought; this is consistent with the record of the paleosols, as well, which indicate only subhumid climates at the wettest (Soreghan et al., 2002). The most unusual thing about these channel and paleosol deposits is their presence within what otherwise appears to be a succession of arid to hyper-arid deposits.

Vegetational temporal patterns across the entire western Pangean region parallel those in areas farther to the east. For example, xeromorphic plants typical of seasonally dry environments have been reported from the Middle Pennsylvanian in the Illinois coal basin (Falcon-Lang et al., 2009; Plotnick et al., 2009), and recently a callipterid has been reported from the Middle Pennsylvanian in this basin, as well (Pšenička et al., 2011). Conifer pollen has been found to dominate assemblages from the late Middle Pennsylvanian in Atlantic Canada (Dolby et al., 2011). These patterns indicate that seasonally dry, subhumid climates alternated on glacial-interglacial scales (Milankovitch) with intervals of humid climate that characterized times of peat formation. At a still larger scale, the early Late Pennsylvanian (Missourian/ Kasimovian) has been characterized as a time of relatively high sea-level and significantly greater climatic dryness across the western and west central Pangean tropics, including Nevada (Bishop et al., 2010), New Mexico (Falcon-Lang et al., 2011a), Utah (Soreghan et al., 2002), and the Applachian Basin (Cecil et al., 1985; Cecil, 1990; Joeckel, 1995; Martino and Blake, 2001; Martino, 2004; Greb et al., 2008). Wetter conditions appear to have returned in the later Late Pennsylvanian (Virgilian/Gzhelian), indicated by the mixed floras and even a rare coal in New Mexico (Krainer and Lucas, 2004), and major coal beds in the Appalachians (e.g., Cecil et al., 1985; Cecil, 1990; Ruppert et al., 1999) with associated typically wetland Pennsylvanian floras (Blake et al., 2002). By the Permian, those floras that are known from the western Pangean regions are uniformly composed of species typical of seasonally dry habitats, with local patches of wetland plants surviving in those parts of landscapes that had semi-permanent, probably ground-water-based, soil moisture (see papers cited above, plus Lucas et al., in press b).

Moving East: North-central Texas

The Eastern Shelf of the Midland Basin of north-central Texas preserves one of the “classic” Permian red beds successions in North America (Figure 9). This area has been the source of numerous studies, mainly in Early Permian vertebrate paleontology, which brought

Figure 9. North-central Texas, Early Permian (Kungurian) red beds deposit, formed in ox-bow lake. Deposits such as these have yielded both flora and vertebrate fauna.

the terrestrial geology of the area into focus (e.g., Romer, 1935; Olson, 1952, Sander, 1989; Nelson et al., 2001; Montañez et al., 2007). Various aspects of paleobotany also have been investigated, mainly systematics (e.g., White, 1912; Mamay, 1967, 1968, 1976, 1986), but also stratigraphy (Read and Mamay, 1964). The Pennsylvanian portion of the section has received less paleontological acclaim, but has been studied in terms of its geology (Moore and Plummer, 1922; Brown, 1967; Feray, 1967; Galloway and Brown, 1973; Hentz, 1988; Tabor and Montañez, 2004) and paleobotany (e.g., Gupta, 1977; DiMichele et al., 2005a). This area was in the southwestern portion of equatorial Pangea during the Pennsylvanian and Permian. As such, the area was subject to atmospheric circulation patterns similar to those affecting areas farther to the paleo-west, in New Mexico and Utah. During the Virgilian (Gzhelian) the wetter parts of climate cycles, presumably driven by glacial-interglacial cyclicity, were usually wet enough for coals to form, though these were generally of low quality, high in ash, thin, and limited in areal extent (e.g., Gennett and Ravn, 1993). These coaly facies become thinner, less widely distributed and ultimately disappear from the stratigraphic succession near the Pennsylvanian-Permian boundary (Hentz, 1988).

The Pennsylvanian-Permian boundary on the Eastern Shelf as defined by conodonts, occurs at about the level of the Saddle Creek Limestone Member of the Harpersville Formation, just below its contact with the Pueblo Formation (Wardlaw, 2005). Farther to the north, where we have studied the paleobotanical succession, the geological section is predominantly terrestrial, with different formational names, but not enough marine limestones to place the Pennsylvanian-Permian boundary accurately with conodont (or any other marine invertebrate) biostratigraphy. However, it can be projected to be in the upper part of the Markley Formation (Hentz, 1988).

Fossil plants are preserved across the Pennsylvanian-Permian boundary, occurring in a variety of facies that preserve both wetland assemblages and those from seasonally dry or better drained substrates. There is very little mixing of these assemblages, based on study of the facies distribution of macrofossils, which appear to have occurred at different stages of glacial-interglacial cycles (DiMichele et al., 2005a). The fossil assemblages are preserved in abandoned channel deposits on landscapes that are represented primarily by paleosols (clastic deposits with a strong pedogenic overprint – see Tabor and Montañez, 2004), or channel-form

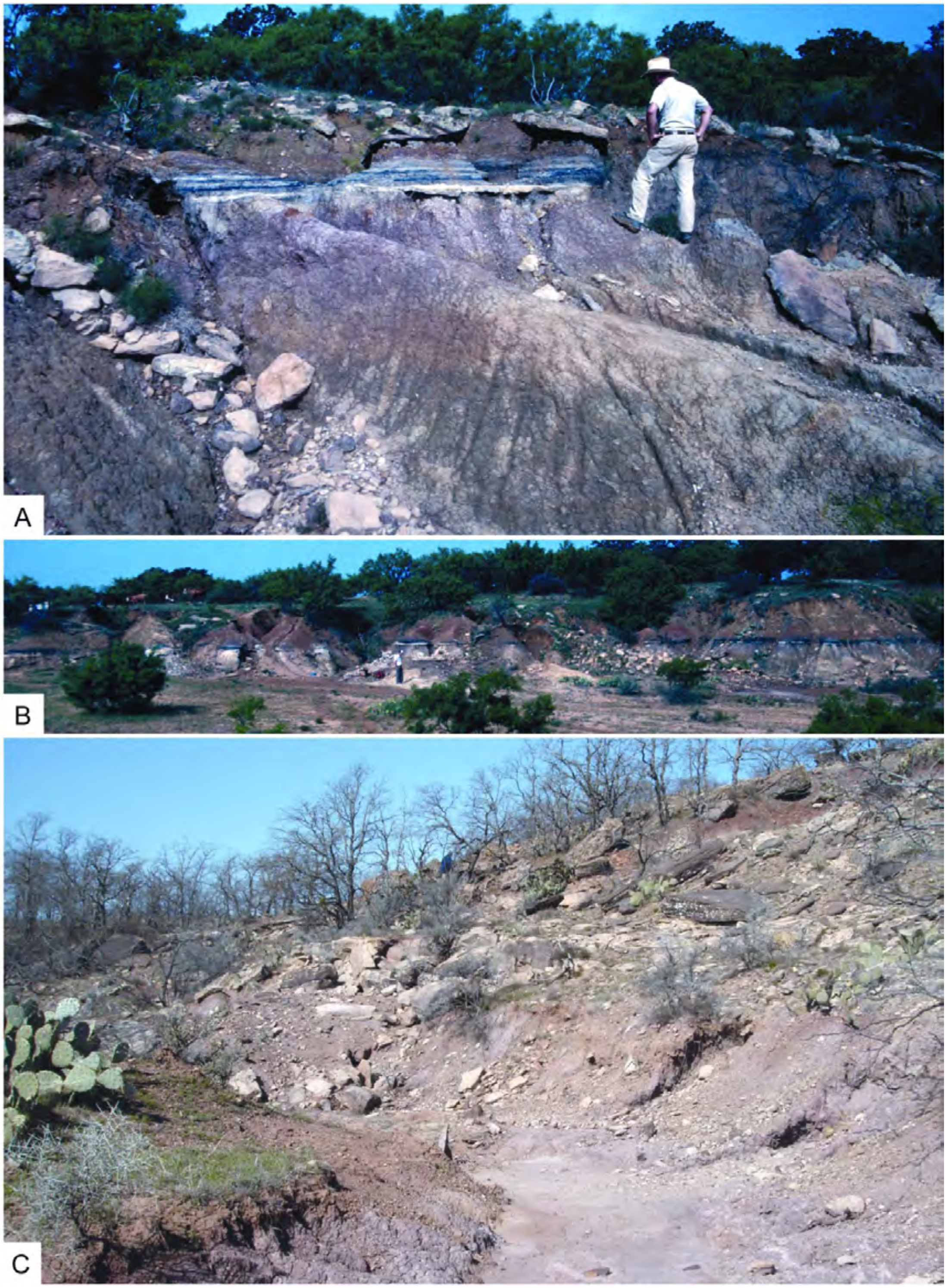

Figure 10. North-central Texas Pennsylvanian and Early Permian age outcrops of the Markley Formation. A—Typical succession of beds from the latest Pennsylvanian. From base: paleosol, quartz-kaolinite siltstone (containing seasonally dry flora), organic shale/coal bed (containing wetland swamp flora), gray siltstones (containing wet floodplain flora), sandstone (represented by float blocks, rarely containing seasonally dry flora). B—Same location as in (A), viewed from a distance. Note the prominent white, quartz-kaolinite siltstone and overlying organic shale bed in the center of the outcrop. C—Earliest Permian plant bearing outcrop, consisting of floodplain siltstone and channel-form sandstone deposits.

sandstones. Plant-bearing deposits occur mainly in association with various coal bed horizons, across which coals/organic shales are discontinuous and variable in thickness and organic content.

A typical outcrop in the lower part of the Markley Formation (Figure 10 A, B) has a distinctive lithological sequence, which is strongly associated with plant biofacies patterns. It must be stressed that this pattern has been observed at multiple outcrops and throughout the Pennsylvanian portion of the Markley Formation, through several cycles, marked by distinct coal-bed horizons. Closer to the Pennsylvanian-Permian boundary, coaly facies are no longer present in outcrops, but the rest of the facies patterns and plant compositional aspects remain the same. These patterns are described by DiMichele et al. (2005a), and from base to top of a typical outcrop they are as follows:

1. A basal paleosol, evidencing wet but well drained conditions, sometimes containing roots that cannot be attributed to specific plant groups. Paleosols may be several meters thick and, throughout the section, evidence a drying trend in the later Pennsylvanian and into the earliest Permian (Tabor and Montañez, 2004).
2. A kaolinite-quartz siltstone bed that may vary in thickness from a few centimeters to over a meter. This bed generally rests unconformably on the upper surface of the paleosol. It contains a flora composed of *Sphenopteris germanica* and walchian conifers, with rare elements including *Charliea*-like pinnules and various pteridosperms. Typically wetland plants have not been identified in this facies. The flora is characteristic of Pennsylvanian seasonally dry climates.
3. An organic-clastic bed that may vary from an organic-rich, finely laminated clay shale to a normally bright-banded coal bed. Where plants are found in this facies, the most common and abundant are typically *Macroneuropteris scheuchzeri*, *Pecopteris* of various species, and *Sigillaria brardii*. This low diversity assemblage represents the typical Pennsylvanian clastic-to-peat swamp flora of flooded substrates with high water tables throughout most of the year. Such beds may vary from less than a meter in thickness to several meters.
4. A sequence of gray to buff siltstone deposited in shallow scours with erosional bases. The siltstones commonly contain a weak pedogenic overprint. Where pedogenesis has not proceeded too far, plant fossils often are preserved in the channel scours. The flora preserved in the fill of any one small scour can vary greatly in species richness, but the overall flora of any given outcrop, consisting of several such subdeposits, is generally the most diverse of any of the plant-bearing facies, consisting of greater than 30 species. These species are principally tree ferns and pteridosperms, typical of Pennsylvanian wetland floras.
5. Sandstone, often many meters in thickness (difficult to measure because of talus formation and vegetational cover) with an erosional basal contact with the floodplain shales may, on occasion, contain plant fossils. Such sands probably are at the base of the subsequent cycle but, because of the nature of weathering in the area, they tend to support hillslopes and occur at the tops of exposed sections. Only rarely have plants been identified in these rocks. Where they have occurred, the plants are cordaitaleans and conifers, both xeromorphic, coniferalean taxa that have been identified as elements of seasonally dry floras. Cordaitaleans are an extremely diverse group, and appear to occur from coastal environments

> (Raymond, 1988; Falcon-Lang, 2005; Raymond et al., 2010) into remote interior areas of tropical latitudes (Falcon-Lang, 2000). However, the appearance of conifers and cordaitaleans in this channel facies is consistent with the appearance of such elements, typical of seasonally dry floras, throughout the Middle and Late Pennsylvanian in coal-bearing rock sequences of the Western Interior basin (Feldmann et al., 2005), Eastern Interior (Illinois) basin (Falcon-Lang et al., 2009; Plotnick et al., 2009), Central Appalachian basin (Martino and Blake, 2001) and the Maritimes area of Canada (Dolby et al., 2011).

The over-riding paleobotanical pattern observed in the Texas deposits is the co-occurrence, at the outcrop scale, of wetland flora and seasonally dry flora (Figure 11), throughout the Virgilian and into the earliest parts of the Wolfcampian. Both vegetation types occupied the coastal plain environment, but they are principally unmixed, occurring in lithologically distinct beds, in stereotypical patterns of succession. Thus, the degree to which these floras overlapped in space and time continues to be an open question. They were certainly likely to have been present contemporaneously in the equatorial region, but did they coexist on lowland landscapes in close spatial proximity, during the latest Pennsylvanian and earliest Permian, as we have surmised from assemblages in New Mexico and Utah? In the case of north-central Texas, the evidence is most parsimoniously interpreted, in our opinion, as indicating they did not share the lowlands contemporaneously. In this area, the wetland plants do not appear to have been confined to channels or channel belts, surrounded by seasonally dry flora. Rather, the confinement of the Texas floras to distinctly different lithofacies, which themselves are of types closely tied to broader indicators of regional climate and sea-level or local base-level, argues for differentiation in space and time.

In light of the climate-rock framework and models described in the introductory portion of this paper, we interpret the floristic and lithofacies patterns in north-central Texas as follows. Coal and organic shale beds reflect the wettest portions of the climate cycles and likely formed during lowstand to late lowstand on a flat lying coastal plain, developing under moist subhumid to humid paleoclimate, differentially in lower areas where standing water was most likely to accumulate for long periods, including channel belts, formed during the earlier phases of sea-level fall. Overlying these organic beds are floodplain deposits, which frequently are in gradational contact with the organic facies. We interpret these as the early phases of sea-level rise, during which climate was still moist subhumid, favorable to development of a wetland flora. These sections contain few or no limestones. So, these low areas of the landscape may have been embayed or served as areas of active drainage during highstand, surrounded by interfluves. From highstand, through falling stages and into early lowstand, paleosols formed on these floodplain sediments, resulting in deep pedogenesis. In addition, shallow channels developed across the landscapes, in which sandstone channel bars were preserved. The climate during these phases, based on the plants, appears to have been seasonal, but still likely dry subhumid. The kaolinite beds have flow features associated with them, and the contained flora is, in most instances fragmentary and evidences at least local transport. We interpret these deposits as representing sediments washed into the channels during early lowstand as rainfall is increasing on the landscape, under the transition from dry to moist subhumid conditions.

The Pennsylvanian-Permian transitional interval in north-central Texas is marked by a strong floristic discontinuity (DiMichele et al., 2010c). Coal beds become progressively thinner and localized in development prior to disappearing entirely in the latest Pennsylvanian,

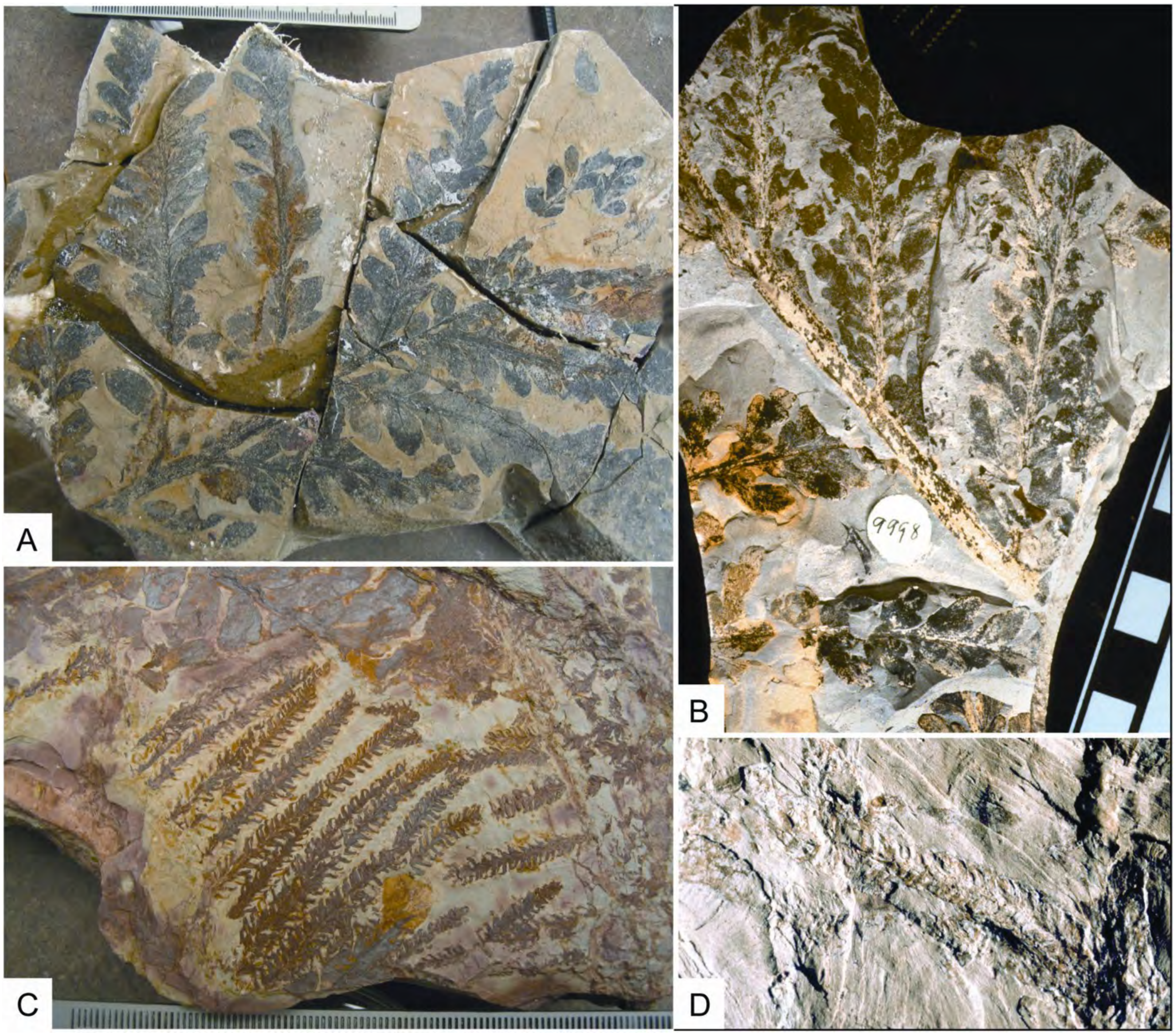

Figure 11. North-central Texas, seasonally dry flora from the Pennsylvanian-Permian Markley and Early Permian Archer City formations. A. *Rhachiphyllum* cf. *schenkii*, callipterid peltasperm frond segment, Early Permian, floodplain siltstone (USNM 536518; USNM loc 40037). B. *Sphenopteris germanica*, quartz-kaolinite siltstone bed (USNM 543965; USGS loc 9998). C. Walchian conifer, Early Permian ox-bow lake deposit (USNM 543966; USNM loc 40027). D. Walchian conifer, quartz-kaolinite siltstone bed (USNM 543968; USNM loc 39998).

suggesting a diminishment of moisture in the wettest phases of glacial-interglacial cycles. In the Permian, there is a change to much simplified lithological patterns on outcrop, and organic beds are lacking (Figure 10 C). Channel sediments, where plants have been identified, are dominated entirely by a flora that resembles that typical of the kaolinite-quartz beds of the Pennsylvanian outcrops, that is: *Sphenopteris germanica*, walchian conifers, and various pteridosperms, but with an admixture of callipterids (such as *Autunia conferta*) and other seasonally dry elements such as cordaitaleans and *Taeniopteris*. This kind of flora remains the most commonly encountered throughout the Archer City Formation, which lies immediately above the Markley and, together with the upper 10 % or so of Markley thickness, is primarily Asselian and Sakmarian in age (Montañez et al., 2007), a time interpreted to be one of major glaciation in the southern hemisphere (Fielding et al., 2008). Montañez et al., (2007) demonstrated strong vegetational tracking of climate changes and dynamics associated with this and subsequent intervals of inferred glaciation and the intervening non-glacial periods. However, we hasten to point out that significant unconformities indicative of prolonged sea level fall associated with long-term, abundant continental ice have not been identified in this region or on the North American craton in general.

Palynology of the north-central Texas section through the Pennsylvanian-Permian boundary (Gupta, 1977) suggests a more gradual turnover than that found in the macrofossils (leading Gupta to place the palynological boundary well above that for either fusilinids or conodonts, at the time his paper was written). These palynological data suggest that the wetter and drier elements of the flora were in reasonably close proximity on the Eastern Shelf, even though this is not supported by the macrofossils, which do not show the patterns of wet-flora/dry-flora co-occurrence seen in the deposits from the more westerly regions of the equatorial belt that suggest spatial adjacency.

In summary, the vegetational transition in north-central Texas, based on macrofossils, appears to be detectable on the temporal scales of both glacial-interglacial oscillations and on the longer scale of the general Pennsylvanian-Permian drying trend. However, the changeover to a more consistently sampled seasonally dry flora is superficially later in Texas, and to the north in Oklahoma (see below), than in New Mexico and Utah, appearing not to have occurred until very near to the Pennsylvanian-Permian boundary. This may, in no small part, reflect a taphonomic sampling bias: wetland deposits, and their associated flora, which may have represented a much smaller temporal fraction of lowland basin occupancy than that of seasonally dry flora (Falcon-Lang et al., 2009; Falcon-Lang and DiMichele, 2010), are more abundant and more easily located by collectors than the seasonally dry flora (often represented either by paleosols or by scattered deposits with poorly preserved fossils), therefore giving the appearance of greater concentration of wetlands on the landscape in time and space than is warranted by fact. Floral samples in the overlying Archer City Formation of Texas, which lacks indicators of climates as wet as or wetter than moist subhumid, are rare and widely distributed in time and space. These floras are typically of the seasonally dry type, which may, in fact, be those of the wettest climate phases. The Markley Formation actually may record only the fact that the wetter parts of glacial-interglacial cycles, such as they were in the latest Pennsylvanian, were simply wetter and more capable of generating widespread wetland landscapes than were similarly much drier wettest phases in equivalent age rocks of New Mexico and Utah. If this is the case, the longer term drying trend in these two areas is less conspicuously offset than would appear, though it is still present.

Northern Oklahoma and Southern Kansas

Understanding of Late Pennsylvanian and Early Permian paleobotany of north-central Oklahoma and adjacent south-central Kansas derives primarily from palynology. This transition occurs in rocks of the latest Pennsylvanian through earliest Permian Wabunsee, Admire, Council Grove, and Chase groups. Macrofossils, although recorded, have not been collected or studied systematically or in their stratigraphic context. In Oklahoma, foliage has been found in cores from the Wood Siding Formation (Wabunsee Group, latest Virgilian) and the Winfield Limestone (Chase Group, Early Permian) (Lupia, 2010), and also has been reported in outcrop in the Doyle Shale (Chase Group) (Chaplin 2010).

The Council Grove and Chase groups, of latest Pennsylvanian through Early Permian age, contain alternating shales and limestones associated with epicontinental sea-level fluctuations, set against a pattern of overall drying through the Early Permian (West et al., 2010). The Pennsylvanian-Permian boundary is placed in the Red Eagle Limestone of the Council Grove Group on the basis of conodonts (Sawin et al., 2006). Abundant evidence of cyclicity consistent with glacial-interglacial drivers has been documented across the Penn-Permian boundary by Olszewski and Patzkowsky (2003), who conclude that eustatic lows were intervals of dry climates whereas eustatic highs were intervals of humid climates, but this may reflect terminological differences from the interpretations presented here. They also note that thin, but persistent coals occur above and below the boundary. Mazullo et al. (2007) also concluded that depositional sequences in these rocks reflect glacial-interglacial drivers, based on examination of isotopic evidence from brachiopods, which they inferred to track changes in ice-volume rather than local ocean temperature.

Previously, two comprehensive palynological sampling programs have studied the Pennsylvanian-Permian boundary interval in this area. Clendening (1970, 1975) investigated Kansas palynology for comparison with his Dunkard studies. Wilson and Rashid (1971) likewise sampled Virgilian through Lower Permian sediments to establish the boundary. In both cases, they concluded that the vegetational change occurred far above the conodont-based boundary assignment in the Red Eagle Limestone, placing it within the lower Chase Group or at its top, respectively. Although lacking in the resolution necessary to detect oscillations, both suggest that Early Permian vegetation was substantially similar to the underlying Late Pennsylvanian. More recently this interval has been reinvestigated (Lupia, 2010), specifically in the context of the conodont-based boundary, and has affirmed these prior large-scale findings as well as observed smaller-scale oscillations in palynological content across the boundary, without a sharp vegetational discontinuity. Rather, wetter-drier phase oscillations are superimposed on a longer-term, coarser scale "drying" trend. The abundance of striate bisaccate pollen, indicative of taxa from seasonally dry habitats (e.g., conifers and peltasperms), is negatively correlated with the abundance of spores representative of wetland taxa (e.g., ferns, horsetails). In the course of these analyses, considerable lateral variation in lithologies was found, suggesting differences in local conditions, not unlike the regional variations found in the Dunkard Group (see below; Cecil et al., 2011; Fedorko and Skema, 2011). One core showed a Virgilian section that was overall quite dark grey and organic-rich, whereas another, from less than 32 km (20 mi) away, showed dominantly red bed shales in equivalent Virgilian strata assuming correct correlation.

The Central Appalachian Basin – Dunkard Group

The Dunkard Group, of the central Appalachian Basin, was located in the western central portion of Pangea during the Pennsylvanian-Permian transition. In this position, it was well inland and backed up against the early phases of tectonic uplift of the Appalachians, which was the source of most Dunkard sediment (Martin, 1998). The occurrence of linguloids in the Washington coal zone (Cross and Schemel, 1956; Berryhill, 1963) suggests that the basin may have had a drainage to the open ocean, but the lack of unequivocally marine fossils in any Dunkard strata strongly suggests that marine waters never actually entered the basin. In fact, the last certain occurrence of marine conditions in the Applachians is the early Virgilian (Gzhelian) Ames Limestone, which has a date securely established by conodonts (Barrick et al., 2008), and lies approximately 100 meters below the base of the Dunkard Group. Dunkard strata are dominantly fine-grained, clay to silt-sized clastic sediments with high mica and low feldspar content, perhaps suggesting a distant source or one poor in such minerals. Common to abundant non-marine limestones, vertic to calcic-vertic, deeply developed paleosols, and evidence of fluctuating water tables indicate a prevalence of subhumid climates, moist and dry, with some periods of greater aridity (Cecil et al., 2011). Coals, indicators of humid climate, are thickest in the lower parts of the Dunkard, where the Waynesburg and Washington coals have been mined commercially. However, above the Washington coal zone, coals tend to be thin and often discontinuous (Fedorko and Skema, 2011). These coals are high in ash and sulfur content (Eble et al., 2011), consistent with their formation under climatic conditions that favored topogenous peat swamps, barely within the climatic and sedimentological window favorable for peat formation (Cecil et al., 1985; Cecil et al., 2011).

Dunkard sedimentation has been described as “cyclic” (Beerbower, 1961, see also Fedorko and Skema, 2011). These patterns are most detectable in the northern portions of the Dunkard Group where facies diversity is highest. On the southern and western margins of the basin, the section consists mainly of interbedded channel sandstones/siltstones and paleosols (Martin, 1998; Fedorko and Skema, 2011). In the deeper portions of the basin, the lithofacies included in this cyclicity indicate the oscillation of regional climate extremes: at the wettest end are the coal beds, indicative of widespread, high-soil-moisture conditions, probably under moist subhumid to humid conditions. At the other extreme are non-marine limestones, indicative of high evapotranspiration and a range of conditions varying from dry subhumid to semi-arid to occasionally arid. Also alternating are conditions that favored widespread vertic paleosol development, often with calcareous deposits, reflective of a strongly seasonal distribution of moisture under subhumid climatic conditions, and deposits of sandstone, siltstone, and mudstone, the grain sizes and geometries of which indicate deposition in standing water bodies of considerable areal extent (Martin, 1998; Cecil et al., 2011; Fedorko and Skema, 2011).

It can be concluded from these observations that the Dunkard Basin was subject to cyclic variations in water table and atmospheric moisture delivery on several different temporal scales. Even at its “wettest” (Waynesburg and Washington coals) there were still intervals of moisture fluctuation and drought of variable duration, sometimes enough to interrupt peat formation and return the region temporarily to high levels of clastic transport (see Cecil and Dulong, 2003, for a discussion of the relationship between climate and sediment transport). Even at its “driest”, the region appears to have been wet enough to support fluvial siliciclastic sediment transport, reflected in features such as frequent clastic partings within limestone, high clastic content of some limestones (making them almost calcareous shales) and the occasional preservation of plants in the limestones themselves, indicative of wet-substrate conditions (specimens of the tree fern foliage *Pecopteris* have been found within the Windy Gap Limestone of the upper Greene Formation).

The Dunkard flora is well established and is characterized overwhelmingly by assemblages of typically Late Pennsylvanian (late Virgilian: Gzhelian) character (see Gillespie and Pfefferkorn, 1979; Blake et al., 2002), typical of wetland habitats. This was clear even from the illustrated macroflora of Fontaine and White (1880), the original description of the flora, from Gillespie et al. (1975), who reinterpreted the flora to some degree, and from the commentaries of White (1936) and Darrah (1969, 1975). Palynological analyses (Clendening, 1972, 1974, 1975; Clendening and Gillespie, 1972) present a similar picture, though they are focused primarily on those rocks representative of the wettest portions of climate cycles (Eble

Figure 12. Northern West Virginia, Brown's Bridge locality from which the original Fontaine and White (1899) callipterids were collected. Site of railroad grade. Modern exposure is heavily vegetated.

et al., 2011), the coals and coal roof shales. In our own collecting, we have found wetland species, particularly pecopterid ferns, in nearly every facies (except clastic paleosols), including limestones, sandstones, the latter representing both high -water deltaic deposits (flat-bottomed sands) and erosionally based channel-form deposits representing low stand or falling stages of base-level, floodplain mudstones, and organic-rich swamp deposits.

The exception to the wetland Dunkard flora is the occurrence of callipterid peltasperms and conifers in some floodplain mudstones and clastic partings in limestones, occurring sporadically (at current levels of stratigraphic resolution) from the Washington coal zone, in the Washington Formation, to the level of the Nineveh coal in the middle Greene Formation (DiMichele et al., 2011) (Figures 12 & 13). These are exceptional occurrences, of which perhaps as many as 10 have been reported (see Darrah, 1975). There appear to be few other taxa in the callipterid assemblages. Most significantly, Darrah (1969, 1975) reports conifers, including what he identified as *Lebachia*, from at least one site. No illustration was provided, and the location of Darrah's collections is unknown to us. In the David White collections made in 1902, and those of Aureal Cross, made in the late 1940s, other taxa, including the pteridosperm *Odontopteris*, calamitalean stems and *Annularia* foliage, are rare. However, most of the collections are small and it is not certain that the non-callipterid material was collected from the same beds as the callipterids (based on examination of the matrix and on what can be gleaned from surviving field notes and notes in collections).

The spatio-temporal distinctiveness of the wetland and callipterid floras most likely reflects environmental control. In keeping with the more widely known and documented occurrences of callipterids (e.g., Kerp and Fichter, 1985; Read and Mamay, 1964) and of peltaspermous seed plants in general (DiMichele et al., 2005b), these plants are likely representative of seasonality of moisture distribution with periods of soil moisture deficit, probably in subhumid climatic regimes. Numerous calcic paleosols, throughout the Dunkard, document climatic intervals with a probable ustic soil moisture regime indicative of an intense dry season for most of the year (Cecil, et al, 2011). And for most such soils, the surface vegetation is not known – it might have been a callipterid-conifer assemblage.

Poor exposure of Dunkard strata (Figure 12) limits our understanding of the environmental context of both the common wetland and rare seasonally dry floras, but much more so the latter. Wetland floras are represented by many more collections and collecting sites than are seasonally dry floras, which provides a "statistically" richer picture of the context of the wetland vegetation, despite the generally limited outcrop exposure. However, the cyclicity of Dunkard lithotypes, and environments they represent (Beerbower, 1961), suggest that the callipterids may (1) characterize one part of any given climate-deposystem cycle, and (2) that there was an increase in climate contrasts in the Dunkard beginning near the time of deposition

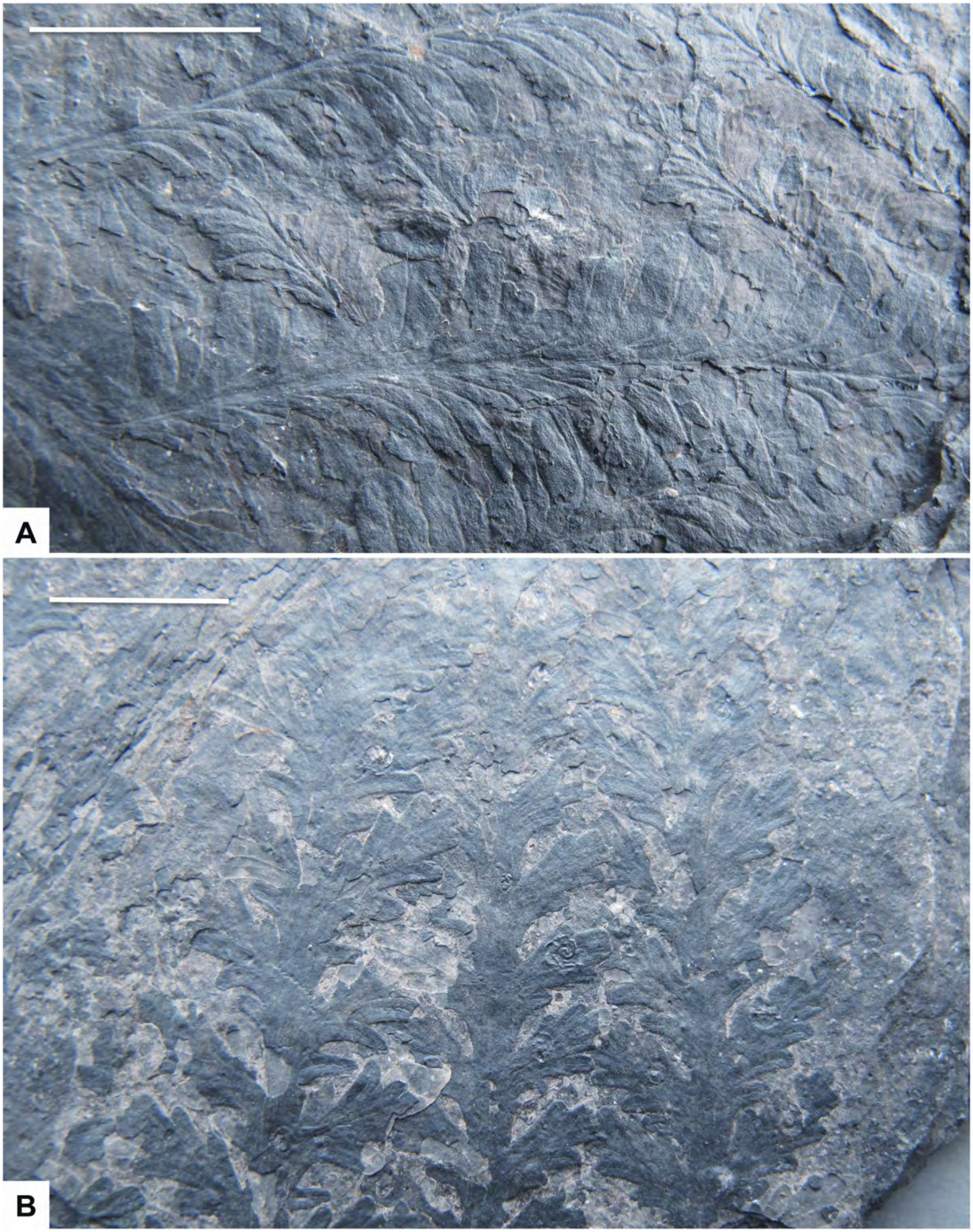

Figure 13. Callipterids from Brown's Bridge locality, West Virginia. Collected by David White, 1902. These species, typical of seasonally dry habitats, were one of the major reasons that Fontaine and White inferred a Permian age for the Dunkard Group. A—*Autunia conferta* (USNM 543957; USGS loc 2926), 4 X magnification. B—*Lodevia oxydata* (USNM 543958; USGS loc 2926), 3X magnification.

of the Waynesburg A coal bed, compared to the oldest portions of the Dunkard and the underlying Monongahela Formation. This climate contrast continued at least through deposition of the lower to middle Greene Formation. Evidence of this increasing contrast between the wetter and drier portions of climate-deposystem cycles is seen as early as the time of formation of the paleosol seat-earth that lies beneath the Waynesburg A coal bed, which is locally a thick, well developed, calcic Vertisol, evidencing strong moisture seasonality with periods of high evapotranspiration. This paleosol is succeeded by a return to humid conditions with the formation of the peat that formed the Waynesburg A coal bed. Paleosols of this type have been found, intermittently, well up into the Greene Formation (such as the exposures on Great House Hill Road, near Wylieville, West Virginia, which is stratigraphically near the position of the Lower Rockport Limestone: Fedorko and Skema, 2011).

There is no definitive marine or radioisotopic evidence by which the Pennsylvanian-Permian boundary can be located within the Dunkard. There are, however, strongly suggestive paleontological and lithological data suggesting that it may lie close to the level of the Washington coal. Such evidence include the occurrence of brackish fauna at that horizon (Berryhill, 1963), consistent with a latest Pennsylvanian marine high stand (Davydov et al., 2010) at that time, non-marine ostracode data (Tibert et al., in press; Tibert, 2011) and tetrapod vertebrate data (Lucas, 2011), both of which suggest a Permian age, possibly beginning around the time of deposition of the Washington coal complex. Thus, the interval within which callipterids appear is, indeed, not an unreasonable candidate for placement of a systemic boundary. Such a placement would be consistent with the early thinking of David White (1904), based on plant fossils (though he later joined I.C. White in considering the entire Dunkard Group to be Permian – White, 1936). That upward diminishment of coaly, or organic-rich, facies throughout the Greene Formation is a similar pattern to that of the other American basins we have discussed. In the Dunkard, the organic facies persist longer than in the basins from the more western regions of the Pangean equatorial belt. This pattern suggests that the wetter end of climate cycles remained moist subhumid to humid longer in a progressive west-to-east direction. As a consequence, a wetland flora remains the most commonly encountered throughout the Dunkard section, even into the Early Permian.

DISCUSSION

There are clear trends in the spatial and temporal patterns of vegetational change across the Pennsylvanian-Permian boundary of the Pangean equatorial region in North America. Wetland species, characteristic of humid and moist subhumid climates, are the most commonly encountered in the terrestrial fossil record of most of the Pennsylvanian, a pattern that has long been recognized. Taxa typical of seasonally dry environments, those not typically associated with organic-rich deposits or in association with physical indicators of humid climates, are characteristically the most commonly encountered plants of Permian age rocks. This pattern appears to be time transgressive. It begins first in the western equatorial regions of Pangea and occurs progressively later in time along the paleoequator to the east, at least on the northern and western side of the Central Pangean mountain belt. As in the Dunkard Group, strata in Western Europe, such as the Lower Rotliegends, which transgress the Pennsylvanian-Permian boundary, have numerous organic-rich deposits, often well into what is interpreted as the Lower Permian, depending on the particular basin and its tectonic setting (see Roscher and Schneider, 2006). These may preserve intercalated wetland and seasonally dry floras, with elements of seasonally dry floras appearing in the Pennsylvanian and, conversely, wetland elements persisting into the Permian (e.g., Remy, 1975; Broutin, 1977; Wagner and Martinez-García, 1982; Wagner, 1983; Kerp and Fichter, 1985; Jerzykiewicz, 1987; Kerp et al., 1990; Popa, 1999; Steyer et al., 2000; Cassinis and Ronchi, 2002; Wagner and Mayoral, 2007; Boyarina, 2010).

Underlying the average vegetational trend is the concept of a progressive "drying" from the Pennsylvanian into the Permian, which is correct at a coarse resolution (see summary in Remy, 1975). However, as resolution is increased, it can be seen that this general drying trend contains a great deal of finer scale climate variation, including that likely to be orbitally forced on the temporal scales encompassed by Milankovitch cyclicity (e.g., Heckel, 2008; Connolly and Stanton, 1992; Rasbury et al., 1998; "stage scale" of Cecil et al., 2011), consistent with glacial-interglacial cycles of the 10^5-year scale. And, on longer time frames, such as that evaluated by Allen et al. (2011), these Milankovich-scale fluctuations in climate can be seen to be superimposed on broader fluctuations in moisture that range in duration from 2 to 6 million years, corresponding broadly to fluctuations in southern hemisphere ice volume (Fielding et al., 2008).

At the glacial-interglacial scale of 10^5 years, increased contrasts can be identified between the intervals of peat formation (humid climate) and those of paleosol formation below the peat beds (subhumid climate) (Cecil et al., 2003; DiMichele et al., 2010c). This began at least by the Middle Pennsylvanian across much of the Pangean tropics west of the Central Pangean mountain belt, which may have simply been highlands at that time, in what is now North America (Roscher and Schneider, 2006). It is reflected in the nature of the fossil-plant assemblages found in association with coals vs. those deposits formed during the drier inter-coal time intervals (Galtier et al., 1992; Falcon-Lang et al., 2009; Plotnick et al., 2009; Scott et al., 2010; Falcon-Lang and DiMichele, 2010). Climate contrasts on the glacial-interglacial scale become even more accentuated during the drier of these intervals, such as the Missourian (early Late Pennsylvanian), where excellently preserved "Permian"-type floras may be found and lithologies record strong contrasts between wetter and drier parts of climate-sealevel-deposystem cycles (Cridland and Morris, 1963; Darrah, 1975; Martino and Blake, 2001; Martino, 2004; Martino and Greb, 2009; Falcon-Lang et al., 2011a; Allen et al., 2011; Lucas et al., in press a).

The physical and biological aspects of these inferred glacial-interglacial oscillations in climate are manifested differently among Pangean depositional basins, depending on regional climatic means, and this affects our understanding of the floras in those respective areas. For example, in western Pangea (New Mexico and Utah), even at those times of wettest climate, peat formation was at best sporadic and generally did not occur. The regional climate system was shifted to the drier end of the "wet-dry" spectrum. Cyclicities can be recognized in the western basins at multiple temporal scales, and they follow the same basic patterns as in more easterly parts of the Pangean tropics: indicators of sea-level change can be identified, there are fluctuations in terrestrial floristic composition associated with these changes, and longer-term changes can be identified associated with changing polar ice volume. The "apparency" of vegetational change, that is our ability to discern such change from the plant fossil record, is, however, strongly affected by regional climate differentiation. The lack of coal in western Pangea removes a focal point for both recognition of and preservation of wetland vegetation in autochthonous and parautochthonous accumulations. As a consequence, the field search images for locating plant-fossil-bearing deposits are very different in a central Pangean coal basin than in areas of western Pangea, where coaly rocks are rare to absent. In the west, we often find plants, after considerable searching and excavation, in rock units that preserve mainly allochthonous material and that formed during portions of the sea-level and climate cycle, such as deltaic deposits formed at highstand or falling stages of sea level, that are considerably different from those represented by coals and the sedimentary rocks immediately associated with them (such as floor and roof shales with which they intergrade). Strikingly, a search for like kinds of lithotypes in coal basins often reveals the same kinds of non-wetland plants as are found in western Pangea, and often in allochthonous assemblages (White, 1912; Arnold, 1941; Cridland and Morris, 1963; Feldmann et al., 2005; Plotnick et al., 2009; Falcon-Lang et al., 2009; Pšenička et al., 2011).

Major changes in the volume of polar ice occur on temporal scales that are considerably longer than those driven by orbital cyclicity (Allen et al., 2011). Glacial-interglacial cycles are superimposed on variations in mean ice volume, and thus on the change in climate state they cause (Cecil et al., 2011). The larger scale changes do not appear to occur rhythmically, as if driven by various combinations of orbital forcing factors, but this is presently uncertain. Such changes appear to have occurred near the Atokan-Desmoinesian (Bolsovian-Asturian, mid-Moscovian) boundary and the Desmoinesian-Missourian (approximately the Moscovian-Kasimomvian) boundary, and to have resulted in threshold-like changes in climate state at those boundaries.

At the Atokan-Desmoinesian boundary, there appears to have been an overall shift toward greater dryness at all phases of glacial-interglacial cycles. This resulted in a shift from an oscillation between perhumid climates during peat formation and moist subhumid climates during the intervening periods, to humid peat-forming climates and dry subhumid climates between periods of peat formation (Cecil, 1990). The result was a change from raised, ombrotrophic peat swamps to planar, minerotrophic swamps (e.g., Cecil et al., 1985; Greb et al., 2002; Eble et al., 2001, 2003), an increase in sulfate and carbonate minerals in the system (Cecil et al., 1985), changed sedimentary patterns (Cecil, 1990; Bertier et al., 2008), and changes in the dominant vegetation of wetland intervals (Peppers, 1996; Cleal, 2007).

Major vegetational change also took place at the Desmoinesian-Missourian (Westphalian-Stephanian in traditional useage, approximately Moscovian-Kasimovian) boundary (Phillips et al., 1974; DiMichele and Phillips, 1996). This vegetational change is closely correlated with, and was seemingly caused by, climatic warming and drying that began earlier in the Middle Pennsylvanian and culminated near the Desmoinesian-Missourian boundary (Cecil, 1990; Phillips and Peppers, 1984), resulting in great diminishment of polar ice (Fielding et al., 2008; Allen et al., 2011) and a high-stand of sea level (Rygel et al., 2008; Heckel, 2008). One of the driving forces of this warming may have been CO_2 (Cleal et al., 1999), which, though not shown definitively for the Desmoinesian-Missourian boundary, has been demonstrated for similar changes in Permian ice volume by Birgenheier et al. (2010), which may serve as a model for this older time interval. Similarly, model studies of late Paleozoic atmospheric composition, ice volume and vegetational feedbacks implicate fluctuations in CO_2 as a major controlling variable (Horton and Poulsen, 2009; Horton et al., 2010). Another exacerbating factor may have been the rise of the Central Pangean Variscan mountain range across Central Europe, which both exposed earlier-deposited coals to erosion and reduced dramatically the area of basinal depocenters (Cleal and Thomas, 2005; Cleal et al., 2009). The Missourian/ Kasimovian warm-dry period transitioned to a seemingly wetter Virgilian/Gzhelian, based on patterns of coal thickness and areal distribution in the central Pangean coal basins (Cecil, 1990), and from patterns seen in parts of the western US, but this phase in particular, as has been discussed in this paper, was spatially quite heterogeneous. The changes at the Desmoinesian-Missourian boundary are instructive when viewed in comparison with Pennsylvanian-Permian boundary. In both cases there is a trend toward drying and perhaps warming through time. However, in the Missourian, this warming and drying appears to be correlated with a significant diminishment in polar ice volume (Fielding et al., 2008) and a distinct global rise in mean sea-level (Rygel et al., 2008). In stark contrast, there is evidence of a major reappearance of ice during the Early Permian, the first of several Permian ice intervals (Fielding et al., 2008; Montañez et al., 2007), though evidence of widespread, long-term sea-level fall has not been demonstrated. Thus, the changes at these two time periods do not appear to be replicates of the same basic kind of global event or set of drivers, and the vegetational consequences certainly were different (DiMichele et al., 2009).

The longest-term climatic trend considered here is that characterizing the general drying beginning in the later Middle Pennsylvanian and continuing throughout the Permian. Difficulties in picking a lithological boundary between the Carboniferous and Permian reflect the gradual, directionally oscillatory, lithological changes that occurred in much of the world between the two Periods – there is no “natural” break, in most instances (see discussion in Wardlaw et al., 2004). This lack of a natural lithological break (lacuna) argues against a global lowstand of sea level, which is consistent with the paleobotanical changes, as described herein. Whereas there certainly is an “on average” difference between a Pennsylvanian tropical flora and one from the Permian, there is always the chance of finding a “Permian”-type assemblage in the Pennsylvanian and vice versa. This has been a point of confusion for many years for paleobotanically-based stratigraphic frameworks. Consider, for example, the remarks of W.C. Darrah in the “Discussion” following Remy’s paper (Remy, 1975), regarding the Garnett, Kansas Missourian flora, which Darrah insisted had to be Permian, or the remarks of Remy (1975) himself, who could not accept explanations of high-frequency climate changes to explain the intercalation of wetland and seasonally dry floras within Pennsylvanian and Permian sections, despite arguing forcefully for strong climatic controls on plant distribution. Such disagreements have continued to the present (e.g., Wagner and Lyons, 1997; Falcon-Lang et al., 2011b). Certainly, the recognition of “xeromorphic” or seasonally dry floral elements as facies fossils, representative of drier climatic settings, has a long history (Elias, 1936, 1970; Arnold 1941).

Long-term drying is the spatio-temporal scale that is most frequently discussed when referring to Pennsylvanian-Permian climatic changes (see, for example, Remy, 1975, who recognizes changes at multiple scales, but focuses strongly on the long-term patterns). It is often discussed, despite clear awareness of the patterns at more resolved temporal scales, as if there is a monotonic trend toward drier and warmer climates, accompanied by a simple vegetational transition. In so doing, an unintended consequence is lack of acknowledgement of the tremendous complexity of this interval, even in an area confined to the low latitudes, encompassing climate and sea level changes, changes in continental positions, the rise and subsequent erosion of mountain ranges, atmospheric circulation patterns and composition, and the interaction of all of these factors. The effects of this multiplicity of variables, many changing in concert at one or more scales of resolution, on the distribution of terrestrial vegetation should be expected to be enormous, and there is no reason to believe that the tropics were not populated by several distinct, barely overlapping species pools, including both plants and animals, that migrated in and out of lowland, basinal settings where the likelihood of preservation was greatest.

This raises the issue of “apparency” in vegetational sampling, and what may be described as a taphonomic megabias (sensu Behrensmeyer and Hook, 1992; Behrensmeyer et al., 2000), that is a large scale, persistent bias in the basic structure of the fossil record. In this case, we use “apparency” to refer to what is most likely to be discovered in the course of normal field activities when prospecting for and collecting plant fossils. For example, there is unambiguous evidence of seasonally dry vegetation living in basinal lowlands beginning at least by the early Middle Pennsylvanian (Atokan/Bolsovian/early Moscovian), from every major terrestrial basin across North America and some in Europe (discussed, with citations, in the preceding paragraphs), that is, not simply in allochthonous assemblages transported into the basins from local “uplands”. Yet, that vegetation is poorly represented and any random sampling of likely host rocks will yield almost invariably a wetland flora. This reflects the strong differences in the preservational conditions during the wetter times of climate-sea level-deposystem cycles in comparison to those when seasonally dry climates prevailed – paleosols may be our best evidence of the plants that once occupied the relatively dry landscapes. Yet, given estimated times of accumulation of peat vs. the development of thick, calcic vertic paleosols, it is not unreasonable to believe that seasonally dry floras were the dominant vegetation of basinal lowlands for extended periods of time during the late Middle and Late Pennsylvanian (DiMichele et al., 2010c), perhaps even occupying these areas for longer than the wetland vegetation that is such an iconic representation of the “coal age” (Falcon-Lang and DiMichele, 2010; Dolby et al., 2011). Conversely, there is ample evidence of the survival of wetland floras well into the Permian, even into the classic Kungurian-age red beds of north-central Texas (DiMichele et al., 2006; Chaney and DiMichele, 2007), demonstrating continued presence on the landscapes, even in the drier parts of equatorial western Pangea.

Asynchonous patterns of vegetational change appear, unsurprisingly, to characterize the Permian itself, as much as the transition from the Pennsylvanian to the Permian. Recent papers on early occurrences of such plants as gigantopterids (Ricardi-Branco, 2008; Booi et al, 2009a) and comiods (Booi et al., 2009b), and certain groups of conifers (Looy, 2007) extend the impression that these plants evolved in tropical envionments and spread out through time, into western Pangea (e.g., Chaney et al., 2009) and still later into such extra-tropical areas as Angara (Mamay et al., 2009). Similarly, early occurrences of typically Mesozoic plants (e.g., DiMichele et al., 2001; Kerp et al., 2006) indicate that there was a tremendous amount of evolutionary and ecological dynamics in the terrestrial landscape that either escapes detection entirely, appears only in brief glimpses as conditions in preservational basins create exceptional windows of opportunity, or appears millions of years after the actual evolutionary origin of the plants and their ecological associations. Thus, the rare occurrence of exotic plant fossils may provide more information about the dynamics of climate than do the abundant wetland floras. Caution is called for when interpreting the fossil record without understanding, or even just an awareness, of the local and regional climatic and sedimentological context of a collection.

CONCLUDING REMARKS

The characterization of changes in terrestrial vegetation across the Pennsylvanian-Permian boundary is literally a problem of "seeing the forest for the trees." One's understanding of it depends on the scale or scales of space and time at which one resolves the data empirically. It also depends on the geographic region with which one is most familiar. Smaller scale, glacial-interglacial oscillations can be detected in most basins along the paleo-equator. However, the patterns and timing of the longer-scale trends – the prominence and areal extent of aridity, say, are spatially patterned and largely time transgressive from west-to-east along the equatorial region. Additionally, given the approximately 10 My of the Pennsylvanian-Permian transition, plant evolution also must be factored into paleoecological analyses. The ultimate conclusion that we offer is not unique, but is similar to that of many who have looked at the Carboniferous-Permian transition, lithologically, faunistically, or floristically: the end points are distinct, but between these different terminal conditions lies a long transition interval, probably as long as either of the better characterized periods. The rationale for a "Dyassic" Period, long ago discussed as a time interval of gradational change between the last coal beds of the Carboniferous and gypsum deposits of the Permian, is clear.

ACKNOWLEDGMENTS

Support for field investigations, provided by the National Museum of Natural History small grants program and the Smithsonian Institution Endowment Funds, is gratefully acknowledged.

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HARPER'S GEOLOGICAL DICTIONARY

AUTOCHTHONOUS - [Gr. Autos - self + chthon - earth, land] Your own personal piece of property, belonging only to you and no one else.