



Published in final edited form as:

Rev Palaeobot Palynol. 2014 December 1; 211: 10–27. doi:10.1016/j.revpalbo.2014.09.007.

Spatiotemporal relationships among Late Pennsylvanian plant assemblages: Palynological evidence from the Markley Formation, West Texas, U.S.A

Cindy V. Looy^a and Carol L. Hotton^{b,c}

Cindy V. Looy: looy@berkeley.edu; Carol L. Hotton: hotton@ncbi.nlm.nih.gov

^aDepartment of Integrative Biology and Museum of Paleontology, University of California, Berkeley, 1005 Valley Life Sciences Building #3140, CA 94720 United States

^bNational Center for Biotechnology Information, National Library of Medicine, National Institutes of Health, Bethesda, MD 20892, United States

^cDepartment of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, United States

Abstract

The Pennsylvanian lowlands of western Pangea are best known for their diverse wetland floras of arborescent and herbaceous ferns, and arborescent horsetails and clubmosses. In apparent juxtaposition, a very different kind of flora, dominated by a xerophilous assemblage of conifers, taeniopterids and peltasperms, is occasionally glimpsed. Once believed to represent upland or extrabasinal floras from well-drained portions of the landscape, these dryland floras more recently have been interpreted as lowland assemblages growing during drier phases of glacial/interglacial cycles. Whether Pennsylvanian dryland and wetland floras were separated spatially or temporally remains an unsettled question, due in large part to taphonomic bias toward preservation of wetland plants. Previous paleobotanical and sedimentological analysis of the Markley Formation of latest Pennsylvanian (Gzhelian) age, from north central Texas, U.S.A, indicates close correlation between lithofacies and distinct dryland and wetland megaflores assemblages. Here we present a detailed analysis one of those localities, a section unusual in containing abundant palynomorphs, from the lower Markley Formation. Paleobotanical, palynological and lithological data from a section thought to represent a single interglacial/glacial phase are integrated and analyzed to create a complex picture of an evolving landscape. Megaflores data from throughout the Markley Formation show that conifer-dominated dryland floras occur exclusively in highly leached kaolinite beds, likely eroded from underlying soils, whereas a mosaic of wetland floras occupy histosols, ultisols, and fluvial overbank deposits. Palynological data largely conform to this pattern

© 2014 Elsevier B.V. All rights reserved.

Corresponding author: C.V. Looy, Department of Integrative Biology, University of California, Berkeley, 1005 Valley Life Sciences Building #3140, CA 94720 United States; looy@berkeley.edu; phone 001-510-642-1607; fax 001-510-643-6264. Both authors contributed equally to this manuscript.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

but reveal a more complex picture. An assemblage of mixed wetland and dryland palynofloral taxa is interpolated between a dryland assemblage and an overlying histosol containing wetland taxa. In this section, as well as elsewhere in the Markley Formation, kaolinite and overlying organic beds appear to have formed as a single genetic unit, with the kaolinite forming an impermeable aquiclude upon which a poorly drained wetland subsequently formed. Within a single inferred glacial/interglacial cycle, lithological data indicate significant fluctuations in water availability tracked by changes in palynofloral and megafloal taxa. Palynology reveals that elements of the dryland floras appear at low abundance even within wetland deposits. The combined data indicate a complex pattern of succession and suggest a mosaic of dryland and wetland plant communities in the Late Pennsylvanian. Our data alone cannot show whether dryland and wetland assemblages succeed one another temporally, or coexisted on the landscape. However, the combined evidence suggests relatively close spatial proximity within a fragmenting and increasingly arid environment.

Keywords

Palaeoecology; Palynology; Environmental change; Pennsylvanian; Texas; Markley Formation

1 Introduction

The Pennsylvanian lowlands in western equatorial Pangaea are characterized by the iconic wetland Coal Age floras, an assemblage of arborescent and herbaceous lycopods, calamites, ferns and seed ferns associated with vast peat deposits (DiMichele and Phillips, 1994, 1996). In contrast, a quite different, apparently contemporaneous flora dominated by waldchian conifers, cordaitaleans, and an array of poorly understood seed plants of uncertain affinity is occasionally glimpsed (Cridland and Morris, 1963; Winston, 1983; Mapes and Rothwell, 1988; Lyons & Darrah, 1989; DiMichele et al., 2010; Falcon-Lang et al., 2011a, 2011b; Bashforth et al., 2014). Based on ecomorphological characters, especially of conifers (Kerp, 1996, 2000) and their sedimentological context (Rueger, 1996; Falcon-Lang et al., 2011b), these gymnosperm-dominated assemblages are believed to represent plants adapted to drier or better-drained conditions. Over the course of the Late Pennsylvanian, these dryland floras become increasingly common until they dominate lowland basins in western Pangaea in the early Permian. Concurrently, the wetland floras contract to spatially and temporally constricted 'wet spots' on the landscape (Rees et al., 2002; DiMichele et al., 2006; Fielding et al., 2008; Montañez et al., 2007; Tabor et al., 2008; DiMichele, 2014). This long-term trend toward aridity is attributed to continental movement accompanied by shifts in atmospheric circulation, orogenic processes and probably most importantly, increased atmospheric pCO₂ (Tabor and Poulsen, 2008; Montañez and Poulsen, 2013).

Increasing aridity is by no means monotonic throughout the Late Pennsylvanian. Superimposed on this long-term trend are short-term climate oscillations driven by orbital forcing (Milankovich cycles) at scales of 10⁶ and 10⁵ years (Heckel, 2008; Tabor and Poulsen, 2008; Pointon et al., 2012; Eros et al., 2012). At high southern latitudes, waxing and waning of glacial ice sheets can be inferred directly from the sedimentological record (e.g., Fielding et al., 2008; Montañez and Poulsen, 2013). At equatorial latitudes in shelf

settings, these glacial/interglacial cycles find expression in cyclothems, repeating packages of coal and terrestrial clastic sediments overlain by marine limestones, as eustatic sea level rose and fell in response to waning and waxing ice sheets (Wanless and Shepard, 1936; Archer, 2009). Although there is general consensus that eustatic sea level change was driven by advance and retreat of high latitude southern ice sheets in response to shifts in atmospheric pCO₂, the precise rainfall and temperature patterns that prevailed during glacial and interglacial cycles remain uncertain. Many models hypothesize that Pennsylvanian interglacials were warm and wet, followed by cooler and drier glacial phases, analogous to climate cycles during the Pleistocene (Feldman et al., 2005; Falcon-Lang, 2004). In contrast, other models posit that interglacials were warm and seasonally arid, whereas glacial phases were cooler and wetter, with major commercial coal formed during maximum glacial advance (Peysner and Poulsen, 2008; Horton et al., 2010; Horton et al., 2012; Cecil et al., 2014). Resolution of this question is beyond the scope of this paper; for our purposes, recognition of cyclicity at short time scales is sufficient.

Similarly, the spatial and temporal relationship between the Pennsylvanian wetland and dryland floral assemblages remains unclear. Peat and clastic swamp floras are usually preserved as autochthonous or parautochthonous assemblages, so their distribution on the landscape is known with a remarkable degree of precision (Gastaldo et al., 2004; Bashforth et al., 2010; DiMichele and Falcon-Lang, 2011). Short and long term taphonomic factors favor their preservation: a high water table and rapid burial in a dysaerobic, acidic environment that discourages decay, within a rapidly aggrading landscape (Gastaldo and Demko, 2011). In contrast, dryland assemblages are at a taphonomic disadvantage because they are buried in sediments exposed to a fluctuating water table, where aerobic conditions foster oxidative attack and microbial decay (Gastaldo and Demko, 2011; Falcon-Lang et al., 2011b). Additionally, during the Pennsylvanian, taphonomic bias against preservation of dryland floras may have been accentuated if they were widespread during times of rapid sea level fall and an erosional regime (DiMichele, 2014).

Two contrasting interpretations of the relationship between wetland and dryland assemblages have been advanced. The first (and older) view posits that wetland and dryland floras were coeval, but that the latter occupied better-drained, upland or extrabasinal sites distant from depositional basins (Chaloner, 1958a; Cridland and Morris, 1963; Pfefferkorn, 1980; Plotnick et al., 2009; Dimitrova et al., 2011). The observed oscillation between wetland and dryland assemblages can be attributed to normal landscape evolution, such as channel migration, stream avulsion and delta switching, i.e., to autocyclic processes (Beerbower, 1964). Climate is often held constant or not considered in this model, although there is no requirement for this assumption. Under an autocyclic model, one would predict some overlap of wet and dry (wetland and better-drained) elements as normal landscape evolution captures wetter or drier parts of the depositional system. A contrasting interpretation views dryland and wetland assemblages as temporally separate, responding to allocyclic shifts imposed by climate change attributable to glacial-interglacial cycles or broader secular trends (DiMichele, et al., 2010, Dimichele, 2014; Tabor et al., 2013). In this interpretation, little overlap between wetland and dryland assemblages should be observed, and one would never expect to see lateral gradation from one type to the other.

Distinguishing between these two hypotheses is not straightforward, especially given the taphonomic bias against preservation in seasonally dry and erosional regimes. Allocyclic and autocyclic processes are by no means mutually exclusive; both likely operate at different times and at different scales. To further complicate matters, sedimentary processes are themselves inextricably tied with climate and vegetation. For example, lower vegetation cover in seasonally dry climates leads to higher erosion and intermittently high (flashy) sedimentation rates (Cecil and Dulong, 2003; Birgenheier et al., 2009; Allen et al., 2011). Humid to perhumid climate with little seasonal variation is characterized by dense vegetation cover, significantly reducing erosion and clastic input (Cecil and Dulong, 2003; Cecil et al., 2003). Significant peat accumulation occurs only when precipitation is greater than evapotranspiration rates for 8–10 months of the year, resulting in a permanently high water table (Cecil and Dulong, 2003).

Outcrops exposed in north central Texas, U.S.A., capture the reorganization of plant assemblages from the Late Pennsylvanian to the Middle Permian in the Midland Basin. Much has been published on the megafloras and sedimentology of this region (e.g., Mamay et al., 1988; DiMichele et al., 2000, 2001, 2004; Tabor and Montañez, 2004; Looy, 2007, 2013, Looy and Duijnste, 2013; Looy and Stevenson, 2014; Tabor et al., 2008, 2013), but very little on the palynology, in large part due to the low preservation potential in the extensive redbeds of the Early Permian part of the sequence (for an exception, see Dickey and Gupta, 1980). In this study we focus on palynology of the latest Pennsylvanian-earliest Permian (Gzezhlian-Asselian) Markley Formation, and compare our data to recent studies focused on megafloras and facies relationships (DiMichele et al., 2005a; Tabor et al., 2013). Palynology offers a source of data complementary to the megafloral record. The small size and resistance to physical abrasion of pollen and spores allows greater dispersal and thus broader sampling of habitats normally not preserved in the sedimentary record, as well as recognition of rarer and more fragile floral elements unlikely to be preserved as megafossils. The presence of palynomorphs in sediments unconducive to megafossil preservation (e.g., certain paleosols) offers an assessment of the vegetation characterizing that lithofacies. Here we present one of the few studies that compares detailed palynological data from both wetland and dryland assemblages in the Late Pennsylvanian. We integrate these data with the sedimentary and plant megafossil records in an attempt to assess the relationships between dryland and wetland flora assemblages and to test two competing hypotheses of plant distribution on the landscape. The preservation of palynologically productive beds in this formation offers a rare window into the broader composition and distribution of plants in a tropical coastal plain setting during the latest Pennsylvanian.

2 Geology and megaflora of the Markley Formation

The Markley Formation was located in the western Pangaeon tropics between 0° and 5° N (Scotese, 1999). Lithostratigraphic correlation from conodont changes within the marine equivalent Harpersville Formation places the Pennsylvanian-Permian boundary near the top of the Markley Formation on a roadcut exposed along US Highway 281, 29.9 km at heading 136.2 from Jacksboro, Texas (Wardlaw, 2005). The formation was deposited in a fluvial-dominated coastal plain setting on the eastern shelf of the Midland Basin, with sediments derived from the Ouachita fold belt to the east and the Wichita-Amarillo and Arbuckle

highlands to the north (Hentz, 1988; Tabor and Montañez, 2004; Tabor, 2007). Its areal extent in outcrop is about 1700 km². The Markley Formation is characterized by a distinctive, repeating package of sedimentation. Each sedimentary package typically consists of a basal paleosol overlain by a light-gray or white, kaolinite-rich siltstone unit between 0.1 and 1 m thick underlying thin coals or organic-rich shales of limited lateral extent. This organic unit is in turn overlain by coarsening-upward mudstones, siltstones and fine sandstones (“heterolithic” beds) and capped by medium to coarse sandstones (DiMichele et al., 2005a; also see Fig. 4 of Tabor et al., 2013). Approximately seven to nine of these repeating sedimentary packages can be recognized within the Formation (W.A. DiMichele, pers. comm., 2011). A distinct suite of plant megafossils characterizes each of these lithological facies. Paleosols (lithofacies 1) contain no body fossils but do display vertically penetrating root casts 3–5 cm in diameter and extending up to a meter below the soil surface, indicating the presence of relatively large trees (DiMichele et al., 2005a). Based on our knowledge of Pennsylvanian plants, the most likely candidates producing these rhizoliths would have been either *Cordaites* or conifers (DiMichele et al., 2005a). Kaolinitic beds (lithofacies 2) contain a distinctive, low diversity megaf flora of walchian conifers, the seed ferns *Sphenopteridium manzanitanum* and *Neuropteris* sp., and sphenopsids *Asterophyllites* and *Calamites*. The organic shale facies (lithofacies 3) is dominated by *Macroneuropteris scheuzeri* and other medullosans, species of Marattiales, *Calamites* and *Sigillaria brardii*, the last surviving arborescent lycopsid in paleotropical Euramerica. The heterolithic facies (lithofacies 4) preserves a somewhat similar wetland assemblage that is dominated by *Pseudomariopteris cordato-ovata* and *Pecopteris* spp., but also includes abundant medullosan seed ferns, *Calamites*, and sphenophylls, as well as rare *Cordaites*, walchian conifers and *Taeniopteris*. Fossils are rare in the sandstone facies (lithofacies 5), but, when present, include conifers, cordaitaleans, and rare *Calamites*, *Neuropteris* and *Pecopteris*. For more details of the megaf flora, see Tabor et al. (2013). Paleosol analysis indicates that there is a long-term drying trend upsection in the Markley Formation. Histosols and ultisols, formed under humid to perhumid conditions, are common in the lower half of the formation but disappear in the upper half (above sandstone 11 of Hentz, 1988). These are replaced by vertisols, which are formed in conditions of fluctuating moisture with four to eight dry months per year (Tabor and Montañez, 2004).

The locality termed ‘Lycopod B’, the focus of this study, occurs in Young County immediately underlying sandstone 10 of Hentz, 1988; also see Fig. 2 of Tabor and Montañez, 2004). It consists of two separate sites, Lycopod B West and East, about 150 m apart, from which a composite section was drafted (Fig. 1). The two exposures together comprise a single typical sedimentary package with a paleosol marking the base and a cap sandstone at the top. The palynologically productive exposure is located at the Lycopod B East site, which has subsequently eroded away. The following description is based on detailed field notes from W.A. DiMichele supplemented by additional field notes from one of the authors (CLH).

The beds at Lycopod B are lenticular, tilting upward at the margin toward the north (Fig. 2). The exposure at Lycopod B East is approximately 3.4 m thick and rests on a paleosol. At the base lies a gray, relatively indurated, kaolinitic siltstone bearing compressions of walchian

conifer branch fragments, up to 10 cm long (bed 1). The bed is obscurely cross-laminated, but becomes increasingly finer grained, planar-laminated and organic-rich in the upper 2–3 cm (bed 2). Fine rhizoliths, several centimeters in diameter, are present in the top of this bed but are rare; otherwise there is no evidence of pedogenesis. A thin layer containing numerous flexible, strap-shaped cuticle fragments of unknown affinities occurs within bed 2. The top of the kaolinitic unit merges gradually into a black, microlaminated mudstone about 3 cm thick containing compressions of *Calamites* and *Sigillaria* (bed 2.5). This unit underlies a thin friable, 18 cm thick coal with vitric streaks (bed 3), and is overlain by a thin highly carbonaceous clay or ‘bone coal’ containing pinnules of *Macroneuropteris scheuchzeri* (bed 4). Above the coal lie a series of medium gray to almost black claystones and mudstones that, together with the coals, comprise the organic facies of this sedimentary package. These clastic units display contorted or obscure laminations, as well as vertical rhizoliths up to 5 mm in diameter, slickenplanes, vertical cracking, manganese coatings, orange mottles and fragments of plant axes (beds 5–11). Fusain fragments occur in beds 10–11. Near the top of the exposure lies a thin, organic-rich paper shale, consisting of highly compressed, unidentifiable plant fragments (bed 12), and overlain by a thin, highly friable coal with vitric streaks at the top (bed 13). The coal is overlain by an organic-rich indurated siltstone (bed 14) containing large compressions of *Sigillaria brardii* and two types of seeds of unknown affinities (Figs. 1 and 2).

The exposure at Lycopod B West correlates precisely with Lycopod B East, and comprises a complete ‘typical’ Markley Formation sedimentary package from paleosol to cap sandstone (Fig. 1). Lycopod B West was not sampled for palynomorphs, but it contains significant suites of plant megafossils. The organic interval is about one half the thickness of the interval at Lycopod B East, and the coals at Lycopod B East grade into organic-rich clastics at Lycopod B West. A unit corresponding to bed 12 of Lycopod B East contains *Macroneuropteris scheuchzeri*, *Calamites* and *Sigillaria*. *Sigillaria* also occurs in a siltstone correlative with bed 14 of Lycopod B East. This fossiliferous siltstone is overlain by a dark gray claystone, which underlies a light, kaolinitic siltstone containing compressions of walchian conifers. This kaolinitic bed, in contrast to the one at Lycopod B East underlies coarsening upward siltstones, mudstones and inceptisols (heterolithic beds) unconformably overlain by a resistant, coarse-grained cap sandstone. The base of the sandstone contains a megafloral assemblage unusual in its abundant cordaitalean leaves, along with rare *Pecopteris* and *Neuropteris ovata* pinnules, and a calamite (Fig. 1).

3 Materials and methods

3.1 Sample collection, preparation and imaging

A trench was dug through the exposure at Lycopod B East to expose fresh sediment (Fig. 2). Palynological samples (sample code LycB90) were collected from each lithologically distinct unit except beds 5 and 11 (Fig. 1 and 2). Approximately 10 g of material for each sample was processed by Global Geolab Ltd. (hydrofluoric and hydrochloric acid maceration, heavy liquid separation and sieving through a 15 micrometer mesh). Palynological residues were strew-mounted in glycerine jelly. Twelve out of thirteen samples were productive. Slides were observed with Nikon Eclipse 80i and Leica DM2500

microscopes. Three hundred grain counts were made, and an additional 200–400 grains were scanned for rare taxa. High-resolution images were taken with the Leica microscope using Differential Interference Contrast, a Plan Apo 63× Oil objective, and a Nikon DS-Fi1 Digital Camera. Extended depth of field (EDF) images were generated using CombineZP (Alan Hadley, <http://www.hadleyweb.pwp.blueyonder.co.uk/CZP/News.htm>). Illustrated specimens are stored in the Paleobotanical Type and Illustrated Collections under the USNM catalog numbers USNM 546150–546189 (see also figure legends).

3.2 Data analysis

A list of pollen and spore taxa and their per-sample abundance was compiled. The initial count data were then reduced by combining certain dispersed pollen taxa that were judged to be likely derived from the same whole plant taxon, in order to create a condensed tally list. Exploratory data analysis was carried out by first examining the composition of each palynological assemblage with respect to abundance, species richness and botanical affinities. Abundance was binned according to the following categories: dominant, 25–100%; abundant, 10–25%; frequent, 5–10%; common, 1–5%; rare, < 1%. Detrended Correspondence Analyses (DCA) was chosen as a data ordination technique to explore the relationship between palynofloral composition and depositional environments. In order to make an informed choice between available ordination techniques, an initial DCA (detrended by segments) was carried out, in which sample scores are expressed in standard deviation. The total lengths of gradient on the first axis were almost 3 standard deviations, justifying the use of an ordination method that assumes a unimodal response of species abundance along environmental gradients (e.g. Correspondence Analysis), rather than methods assuming a linear response model (e.g. Principal Component Analysis). The detrending method in the analyses was based on 26 segments. The data set utilized 30 taxa or groups of taxa with an abundance of 2% or higher in at least one of the samples. Rarer taxa were combined with other taxa from the same plant group, except for *Nuskoisporites* and *Potonieisporites*, which are of particular ecological interest. The DCA was carried out using PAST 3.02 software (Hammer et al. 2001). Palynofloral diversity of all samples was summarized in two metrics that reflect two important aspects of diversity: simple diversity (S) to express taxon richness (or the number of taxa encountered in a subset of 300 palynomorphs), and equitability (E_H) as a measure of evenness. The latter is the Shannon index for entropy divided by the natural logarithm of the simple diversity. It is calculated as follows:

$$E_H = - \left(\sum_{i=1}^S p_i \ln p_i \right) / \ln S$$

where p_i is the proportion of individuals of the i^{th} species in the total number of specimens, and S is the number of taxa in the sample.

4 Interpreting plant distribution from dispersed pollen and spores

4.1 Botanical affinities of pollen and spores

Reconstructing landscapes from dispersed pollen and spores requires knowledge of the affinities of the parent plants. For Pennsylvanian wetland species, affinities of many pollen/spore taxa are well known at the family or ordinal level, e.g., Sigillariales, Chaloneriaceae, Medullosales, Sphenophyllales, Calamitales, Marrattiales, Tedeleaceae, Gleicheniaceae (Table 1). Parent plants for dryland taxa, because of their relative rarity, are much more poorly understood. However, some generalizations can be made. Monosaccate prepollen (*Potonieisporites* and *Nuskoisporites*) can be connected with confidence to walcchian conifers (Table 1; Poort et al., 1997). Non-taeniate bisaccate pollen (*Falcisporites*, *Pityosporites*) has been attributed to Permian peltasperms (Zavialova and van Konijnenburg-van Cittert, 2011). *Vesicaspora* is well established as pollen of Carboniferous Callistophytae (Millay and Taylor, 1979; Rothwell, 1981), but has also been associated with Angaran Permian and Triassic peltasperms (see review in Zavialova and van Konijnenburg-van Cittert, J.H. 2011). Either the *Alisporites/Falcisporites* complex or *Vesicaspora*, or both, may represent spores of local peltasperms (DiMichele et al., 2005b; Table 1 and references therein). This association is plausible, as peltaspermals may be related to or possibly even descended from callistophytes (Hilton and Bateman, 2006; DiMichele et al., 2013). Several taeniate saccate pollen (*Protohaploxylinus*, *Striatoabietites*, *Hamiapollenites*) and taeniate non-saccate pollen (*Vittatina*) have not been associated with parent plants in the Pangean tropics. Taeniate bisaccates are characteristic of the Southern Hemisphere order Glossopteridales (e.g., *Protohaploxylinus*, *Striatopodocarpidites*; Table 1; Zavada, M.S., 1991; Lindström et al., 1997). However, no glossopterid megafossil has ever been reported from the equatorial lowlands, so Glossopteridales are considered highly unlikely sources for taeniate pollen in the Markley Formation. Taeniate pollen (*Protohaploxylinus*, *Vittatina*) has been found in association with the Upper Permian Angaran peltasperm *Tatarina* (e.g., Gomankov and Meyen, 1986). Thus, peltasperms may have been one group that produced taeniate pollen in the Late Pennsylvanian and Early Permian of tropical Pangea, although there is no direct evidence of this. *Colatisporites decorus* is another problematic taxon. It bears a strong resemblance to *Angulisporites intonsus* Wilson 1962, originally described as a spore by Williams in Neves et al. (1973) and treated as such by Dolby et al. (2011). However, it has a pseudoalveolar outer layer and bears a strong resemblance to *in situ* spores in ovules of *Lyginopteris* (Retallack and Dilcher, 1988). We treat it here as a likely seed fern of unknown affinities.

Two factors complicate the interpretation of parent plant from dispersed pollen and spores. The first is rampant homoplasy in palynomorph morphology, especially in taxa with simple morphology. For example, the morphotaxon *Granulatisporites* was produced at various times by most of the major vascular plant clades (lycophytes, monilophytes, seed plants) (Table 1). The megaflora in the Markley helps constrain possible candidates; in this case, the source plant for *Granulatisporites* was probably some kind of fern. Another, more problematic example comes from the smooth monolete spore *Laevigatosporites*, produced by both Marattiales and Sphenophyllales. Generally, smaller forms less than about 30 micrometers are attributed to Marattiales and larger forms are attributed to Sphenophyllales;

however there is some overlap in size distribution between these two orders (Ravn, 1986). A second confounding factor is the evident inflation of dispersed spore and pollen species and genera, given the diversity of dispersed morphotaxa that can be recognized in a single sporangium or pollen (e.g., Zavada, 1991; Lindström et al., 1997; Bek and Pšeni ka, 2001). For these reasons, we have adopted a conservative approach to palynomorph species circumscriptions, but it should be borne in mind that some degree of error in taxonomic assignments will remain in any paleoecological analysis using dispersed pollen and spores.

4.2 Pollen and spore taphonomy

Taphonomy of dispersed pollen and spores must be considered before they can be used as proxies for plant assemblages in ecological space. Pollen and spores are generally deposited as silt-sized particles, so they are usually not present in coarse grained sediments such as sandstones or in very pure claystones (Traverse, 2007). The distribution and abundance of pollen and spores in sediments is affected by numerous factors, including abundance and height of parent plant, pollen productivity and wall thickness, phenology and mode of pollen/spore dispersal, canopy structure, prevailing wind patterns and air currents, rainfall patterns, position on the landscape relative to depositional centers, and environment of deposition. Trees that are heavy pollen or spore producers, such as Marattiales (tree ferns), will be particularly overrepresented in a given sample. Common taxa will overwhelm rare taxa, species growing close to a catchment area will be more abundant than those distant from the basin, and taller plants will disperse their spores or pollen farther than plants of low stature. Herbaceous ferns, for example, tend not to disperse their spores far from where they are growing. How pollen or spores are distributed also plays a role in pollen productivity and distribution. It is often assumed that all Pennsylvanian plants were anemophilous, but the large size of pre-pollen of Medullosaceae (200–600 micrometers) suggests zoophily (Taylor and Millay, 1979; Labandeira, 2000; Schwendemann et al., 2007), or perhaps hydrophily (DiMichele, 2014). Zoophily could explain the apparent underrepresentation of Medullosaceae in the pollen record relative to their abundance in megafossil assemblages, because zoophilous plants tend to produce less pollen. The structure of the canopy also affects pollen and spore distribution, since open canopy allows dispersal by air currents over a greater distance. Coal swamps dominated by Marattiales are thought to have possessed closed canopies (DiMichele et al., 2009), which may be one of the factors accounting for the hyperabundance of tree fern spores in many samples. Data on spacing of trees in dryland habitats are limited; however, what little evidence exists suggests a relatively open canopy (Falcon-Lang et al., 2011a; Bashforth et al., 2014). In any case, plant cover in general tends to be significantly lower in drier environments, because water is the single most important physiological constraint for land plants, so it is reasonable to suppose that canopy in dryland environments was not as dense compared to wetland habitats.

Knowledge of facies type is also critical to making accurate ecological extrapolations from dispersed palynofloras. As a general rule, depositional environments with little or no clastic input, such as peat or carbonaceous mudstones, will represent primarily spores or pollen carried by wind from vegetation growing in or near the periphery of the depositional site (Bunting, 2008). These kinds of depositional environments will more closely resemble megafossil assemblages (Nichols, 2005). In contrast, sediments deposited at the mouth of a

large river can potentially include palynomorphs drawn from great distances and highly varied environments (as a modern example, pollen from North Dakota can be carried downstream for hundreds of kilometers and deposited at the mouth of the Mississippi River (Traverse, 2007)). In general, pollen/spore assemblages, especially those derived primarily from water lain deposits that include a mixture of sediments eroded and re-deposited from stream banks, are time-averaged, in contrast to most megafloral assemblages, which represent ‘snapshots’ or near instantaneous events (Burnham, 1993; Wing and DiMichele, 1995).

5 Results

5.1 Palynology

Two endpoint assemblages may be recognized among the samples. Assemblage I occurs in the organic facies (LycB90-3-14), and is dominated by characteristic Late Pennsylvanian wetland taxa (Fig. 3, Plates 1 and 2, Table 1). Spores of Marattiales (e.g., *Cyclogranisporites*, *Punctatisporites* spp., *Punctatosporites* spp., *Laevigatosporites globosus*, *Thymospora* spp. and *Verrucosisporites microtuberosus* (Plate 1, Figs. 16–20) are consistently present and collectively are abundant to dominant. Arborescent lycopsids are represented by low levels of *Crassispora kosankei* (*Sigillaria brardii*), *Endosporites globiformis* (*Chaloneria* spp.), as well as *Cadiospora magna* (*Thomasostrobus*, possibly Sigillariales) (Plate 2, Figs. 1–3). Spores of *Calamites* (*Calamospora* spp.) as well as Sphenophyllales (e.g., *Laevigatosporites medius* and *L. desmoinesensis*) are abundant in most of the organic facies (Plate 1, Figs 3–6). Herbaceous ferns display considerable diversity, although usually in low abundance (Plate 1, Figs. 7–15). Cordaitalean prepollen (*Florinites* spp.) varies from common to abundant (Plate 2, Figs. 4–7). Pollen or prepollen of other seed plants, such as the medullosan seed fern *Schopfipollenites*, are rare (Plate 2, Fig. 14). Conifer prepollen such as *Potonieisporites*, *Nuskosporites* and other non-taeniata bisaccates and pseudosaccates occur sporadically at extremely low abundance (one or two grains on a slide) throughout the section.

Within the organic mudstones, two samples, LycB90-8 and 9 (from beds 8 and 9) are somewhat anomalous in displaying low diversity and possessing unusual taxa or unusually high abundance of certain taxa. Sample 8 is strongly dominated by the marattialean tree fern spore *Cyclogranisporites minutus* and a complex of spores resembling *Punctatisporites punctatus*, *P. obesus* and *P. flavus*, many with anomalous germination apertures (Fig. 3). Presumed sphenophyte spores (large *Laevigatosporites* spp.) are common, whereas other fern and seed fern spores are subordinate. Sample 9 is characterized by unusual taxa, especially the putative seed fern taxon *Colatisporites decorus* and seed plant *Illinites unicus*. *I. unicus* (Plate 2, Fig. 18) is a taeniata bisaccate suggesting a phylogenetic relationship to Permian forms, but it is locally common in Late Pennsylvanian wetland floras (Peppers, 1996).

Assemblage II occurs only in the kaolinitic siltstone at the base of the exposure (LycB90-1) and comprises a markedly different flora compared to the rest of the section (Fig. 3). Dominants in this assemblage include pollen of seed ferns such as the non-taeniata bisaccates *Falcisporites* and *Alisporites*, and species of the pseudobisaccate genus

Vesicaspora (Plate 2, Fig. 13, 15–17). Species of *Potonieisporites* (Plate 2, Fig. 8–12), representing walchian conifers, are abundant. Diversity and abundance of spores in this assemblage is low, and only species of *Cyclogranisporites* (Marattiales) are common. Sphenophyte spores (*Calamospora* and *Laevigatosporites*), lycopsid spores (*Cadiospora*, *Crassispora*, and *Endosporites*), and cordaitalean prepollen (*Florinites*) are all rare. Most of the less common taxa found in Assemblage I are absent.

A mixed assemblage that includes taxa from both Assemblage I and II is found in samples from the top of the kaolinic siltstone immediately underlying the first coal bed (samples LycB90-2 and 2.5 from beds 2 and 2.5; Fig. 3). Just as in Assemblage II, the non-taeniate bisaccates *Falcisporites* and *Alisporites* are dominant. Prepollen of walchian conifers is abundant and includes *Potonieisporites* and *Nuskoisporites*. A pseudobisaccate or monosaccate form that we term here *cf. Sahnisporites* may also represent a conifer, based on its morphological similarity to *Potonieisporites*. Most unexpected, several grains of *Protohaploxylinus* occur in sample LycB90-2—this becomes much more common in the Permian of north Texas and elsewhere but is extremely rare in the Pennsylvanian (Peppers, 1996). The proportion of lycophyte, sphenophyte, and marattialean tree fern spores, and cordaitalean prepollen, however, is much higher compared to Assemblage II; in this respect, the mixed assemblage more closely resembles Assemblage I (Fig. 3). The sphenophyll *Columinisporites ovalis* is common in these two samples, in marked contrast to its rarity elsewhere in the section (Fig. 3).

Per sample taxon richness ranges from 30 to 55 taxa (Fig 4). Most of the samples in the organic facies display moderate evenness and diversity. Exceptions are samples 8 and 9, which display low species diversity and low evenness. Sample 2 combines the highest diversity (55 taxa) with high evenness and sample 2.5 displays moderate diversity and evenness. The assemblages with the highest number of taxa also display high equitability, whereas the less diverse samples lack evenness. Compared to the other samples, Assemblage II has low mean diversity, coupled with the lowest evenness.

5.2 Ordination analysis

Ordination of palynological abundance data against sample (i.e., bed) shows clearly that samples are arrayed along Axis 1, which accounts for 26.4% of the variance in the data (Fig. 5). Axis 2 accounts for another 10.5% of the variance in the data. The taxa that drive these loadings are outlined in convex hulls of color for visual clarity. Fern spores, primarily those of Marattiales but also including herbaceous ferns such as *Triquitrites* (Gleicheniaceae), as well as *Florinites* prepollen (Cordaitales) occupy an area in ordination space on the central to left side of Axis 1 where they peak in abundance. Seed plant peak abundances, except for Cordaitales, are strongly clustered on the positive side of Axis 1, with none having scores lower than about 200. Sphenophytes display greater range along Axis 1. Notably, *Columinisporites ovalis* (Sphenophyllales) lies well within the seed plant cluster; this species is one of the few spore types to persist into the Permian. Perhaps surprisingly, because lycophytes tend to occupy the wettest habitats in many Pennsylvanian wetland assemblages, lycophytes here lie outside the cluster formed by *Florinites* plus fern spores.

Like *Columinisporites ovalis*, these lycophyte taxa represent forms that persist into the Permian.

6. Discussion

6.1 Lithofacies interpretation of Lycopod B

Ecological inference rests on a detailed understanding of the environments of deposition in which the palynofloras and megafloral assemblages are preserved. The contact with the underlying paleosol at Lycopod B is buried, so its composition and geometry of overlying beds is uncertain. However, typical paleosols in the lower Markley Formation underlying coal/carbonaceous shales correspond to Pedotype B of Tabor and Montañez (2004), representing paleovertisols developed on sites of low relief during periods of sedimentary stasis in a humid to subhumid climate experiencing some periodic drying. Comparable kaolinite/organic sedimentary packages elsewhere in the Markley Formation display an erosional contact with the underlying paleosol and are shallowly trough-shaped (Tabor et al., 2013). The upward tilt of the kaolinite unit and overlying beds at one end of the exposure at Lycopod B East suggests that this outcrop exhibits a similar geometry.

Throughout the Markley Formation, kaolinite units closely resemble underlying paleosols in mineralogical composition, indicating that they were eroded from the paleosols (Tabor et al., 2013). Kaolinite beds indicate a high degree of leaching and formation in hot, humid climatic conditions. Obscure cross laminations and absence of pedogenesis indicates both kaolinite beds at Lycopod B were deposited relatively rapidly, probably as sheet wash or channel overflow. Fining upward, fine laminations and increased organic content at the top of the kaolinite at Lycopod B East indicate settling out in a brief ponding interval. The bulk of sedimentation of the kaolinite at Lycopod B East carries allochthonous elements such as small branches of walcian conifers, but the top includes parautochthonous elements, including plants such as *Calamites*. In the Markley Formation, almost all kaolinites underlie organic rich facies (Tabor et al., 2013). Exceptions to this rule include the kaolinite within heterolithic beds at Lycopod B West, and in similar deposits at two older localities. This close correlation between kaolinitic units and overlying organic beds implies a genetic association between the two units: once deposited, the clay rich kaolinite created a poorly drained aquiclude upon which a wetland could form (Gardner et al., 1988; DiMichele et al., 2006; Gastaldo, 2010).

Thinning of beds and grading of coals into clastics from Lycopod East to Lycopod West indicate that the organic facies was, like other lower Markley Formation organic-rich beds, a spatially limited, poorly drained wetland fill within a relatively shallow, broad channel, probably a fluvial channel cutoff. Thin peats formed at the base and top of the organic facies at Lycopod B East, indicating a high water table, but there is evidence of fluctuating water table within this unit. Both coals contain vitrain, representing degraded woody material, likely derived from degraded sheets of lycopsid bark (here, almost certainly *Sigillaria*) (Boyce et al., 2010). Extremely sluggish streams or occasional sheet flow into the swamp were probably responsible for the deposition of beds 6 through 12. The high organic content, good palynomorph preservation, gley color and limited pedogenesis in these beds indicate deposition in water-saturated, dysaerobic and acidic conditions. Beds 3 through 7

correspond to Pedotype A of Tabor and Montañez (2004), interpreted as a histosol formed under conditions of poor drainage and low sedimentation. Bed 8 displays evidence of better drainage and increased exposure to oxidation, from the presence of orange mottles, manganese/iron coatings, and iron oxide nodules, indicating a drop in water table and partial drying. Beds 9 through 14 become increasingly organic-rich, culminating in another thin coal in bed 13, and display other signs of immature pedogenesis and a high water table. The presence of fusain in beds 10–12, however, indicates periods of drought on the landscape with consequent wildfires, indicating increasing seasonality.

The heterolithic beds above Bed 14, marked by a coarsening upward set of shales, mudstones, fine sandstone channels and immature paleosols, indicate a shift toward more active sedimentation on a low energy, regressive coastal flood plain. Collectively the heterolithic beds are considered floodplain deposits. Coarsening up sedimentation indicates movement from an initially more distal position on the floodplain to a proximal position relative to the channel. The cap sandstone represents a channel of unknown size at Lyopod B West. At other localities, channels range from a few meters to a few tens of meters thick and contain fine to coarse and occasional conglomerates, indicating low to relatively high stream energies. Channel cutting and sand deposition is probably contemporaneous with formation of paleosols, so cap sandstones and paleosols likely represent part of the same, more active sedimentary phase in the sedimentological cycle (Tabor and Montañez, 2004, Tabor et al., 2013).

6.2. Palynological interpretation of Lycopod B

Since seed plants as a group possess reproductive traits such as enclosed gametophytes and conductive tissue that are advantageous in water limited conditions compared to pteridophytes as a group, water availability is reasonably interpreted as the primary factor affecting Axis 1 (Fig. 5). Samples in the organic facies lie toward the left (wet) side of the graph, with considerable spread, while the seed-plant basal kaolinite (Assemblage II) lies to the very right of the graph, on the 'dry' end of Axis 1. The two mixed assemblages lie between the kaolinite and the organic facies, and clearly represent some kind of transition between dryland and wetland assemblages, or a mosaic of wetland and dryland communities (Fig. 5). Within the organic cluster, which represents Assemblage 1, sample 9 compositionally most closely resembles the dry and mixed floras, and lies close to them along Axis 1.

The ordination analysis clearly shows the existence of strong phylogenetic niche partitioning in the Lycopod B flora (Webb et al., 2002). Ferns and cordaitaleans form the core of the wetland community (Assemblage I). Lycophytes lie between the wetland and dryland floras and represent Late Pennsylvanian, more xerophytic survivors within this clade. Hygrophilic lycophytes such as Lepidodendrales mostly disappeared by this time (DiMichele et al., 2009). Sphenophytes display a fairly broad range along the moisture gradient, with *Calamites* and certain Sphenophyllales displaying a greater affinity for wetland habitats. Seed ferns and walchian conifers cluster along the dry side of the moisture gradient, with the putative seed fern *Colatisporites decorus* and seed plant *Illinites unicus* and lying somewhat closer to the wet side of the moisture gradient. These taxa both represent Pennsylvanian

holdovers, occupying drier parts of the wetland assemblage. An important element that is missing from this discussion, because of its rarity in the pollen record, is *Schopfipollenites* (Medullosales), which should lie well within Assemblage I based on megafloral data (see next section).

The factor that accounts for Axis 2 is likely disturbance. Inspection of the data suggests that abundance of *Florinites* is driving the spread along the axis (Fig. 3). *Florinites* occupies the most negative space in the graph, and is widely separated from a number of Marattiales taxa, both suggesting that tree ferns and Cordaitales occupied different ecological niches within the wetland community. Evidence from other sources indicates that some species of Marattiales replaced Lepidodendrales in the wettest parts of the wetland habitat in the Late Pennsylvanian, but that as a group they occupied a wide range of wetland habitats (DiMichele et al., 2009). Cordaitales, on the other hand, occupy a wide range of wetland to well-drained, but not dryland habitats (Falcon-Lang and Bashforth, 2005; Bashforth et al., 2014). However, they tended to occupy more stable habitats within fluvial systems, in contrast to Marattiales, which tended to occupy more disturbed habitats, although not as pioneering species (Bashforth et al., 2010, 2011).

Low species evenness and richness may be caused by constraints on biomass production (stress), disturbance (biomass destruction) or as evidence of a climax community (e.g., Begon et al., 2006). Samples LycB-90 1 and 8 are both relatively poor in taxa, and display by far the lowest equitability. Interestingly, these two lie at opposites ends in the palynofloral compositional spectrum, as shown in the DCA ordination (Fig. 5). Based on the composition of Assemblage II, sample 1 likely represents a homogeneous gymnosperm dryland community with relatively few spore producing taxa present. The low species richness in sample 8 may reflect disturbance, as this bed displays the highest degree of both pedogenesis and oxidation within the organic facies.

6.3 Comparison of palynofloral and megafloral assemblages

Higher taxonomic diversity in the palynofloras indicates that they capture a larger fraction of the actual floristic diversity, compared to megafossils. For example, palynology reveals a much larger variety of herbaceous ferns, which are absent in the megafossil record, as well as the consistent presence of cordaitaleans throughout the section. Cordaitaleans tend to be underestimated in the megafossil record due to the difficulty of distinguishing cordaitalean leaf fragments from rachis fragments (Tabor et al., 2013).

A certain degree of taxonomic congruence between megafloral and palynofloral elements exists in both organic and kaolinite facies, but it is greater in the organic facies. Megafossils recognized in the organic facies at both Lycopod B West and Lycopod B East include *Sigillaria brardii* (*Crassispora kosankei*), *Calamites* spp. (*Calamospora* spp.), *Pecopteris* spp. (numerous spore taxa), and *Macroneuropteris scheuchzeri* and *Neuropteris ovata* (*Schopfipollenites*). These are typical elements of the wetland flora and are largely reflected in the palynological record. The most important exception to this is *Schopfipollenites* (Medullosales), which is quite rare in the pollen record. In contrast, *Macroneuropteris scheuchzeri* is the dominant species in the organic facies (Tabor et al., 2013). Numerically, spores of Marattiales are dominant throughout the organic facies, with sphenophylls,

Calamites and *Sigillaria* very much subdominant. Marattiales are known to be prolific spore producers, so palynological abundance is unlikely an accurate representation of the composition of this wetland. Nevertheless, the palynoflora indicates that other groups were at least as important components as medullosan seed ferns, in contrast to by the megafloral record, which indicates that medullosans (*Macroneuropteris scheuzeri*) was dominant (Tabor et al., 2013)..

In contrast, megafloras and palynofloras are relatively incongruent in the kaolinitic unit at Lycopod B. In part, this is due to more incomplete knowledge of spore/pollen affinities of the dryland assemblage. Only walchian conifers and *Calamites* occur in the kaolinite bed at Lycopod B East (as well as another kaolinite bed in Lycopod B West) (Fig. 1), although this is no doubt due to limited sampling. Comparable kaolinitic units elsewhere in the Markley Formation typically contain low diversity floras dominated by *Sphenopteridium manzanitum* (?*Lyginopteridaceae*). They also include walchian conifers, Medullosales and Calamitales (Tabor et al., 2013). Only *Potonieisporites* and *Calamospora* represent common elements in both the palynoflora and megaflora. Palynologically, the dominant elements in the kaolinite bed are non-taeniate bisaccate and pseudobisaccates which may represent peltasperms, callistophytes or perhaps even callipterids; these taxa are rare or absent in the kaolinite megafloras. The affinities of *Sphenopteridium manzanitum* are uncertain, and its pollen is unknown. If it is indeed lyginopteridalean, a connection with *Colatisporites* would be possible, but *Colatisporites* does not occur in the Lycopod B East kaolinite bed (although it does occur in drier assemblages in the Lower Permian of Texas (Looy and Hotton, unpublished data). Marattiales are diverse but at low abundance in the palynoflora, and are represented in the megaflora by rare *Pecopteris* pinnules. In this instance, megaflora and palynoflora agree. Walchian conifer prepollen (*Potonieisporites*, *Nuskoisporites*, and possibly cf. *Sahnisporites*) and seed fern pollen (*Alisporites/Falcisporites*), occurs throughout the wetland facies at very low abundance. These taxa are not reflected in the megafossil record at all. Similarly, *Florinites* (Cordaitales) is common to dominant throughout the organic facies and rare in the kaolinite unit, but occurs in only one megaflora in Lycopod B West. This agrees with other evidence that cordaitaleans were important elements of the vegetation in both wetland and better-drained riparian habitats (Bashforth et al., 2014). *Florinites* reaches its highest abundance in bed 14, which contains no megafloral remains of Cordaitales. *Sigillaria* occurs in this same bed, but no *Crassispora* was observed in the palynoflora at this level. These incongruities caution against reading too much into absences in either the palynoflora or megaflora at a given level, because incomplete sampling and imperfect preservation can and do distort floral content in a given bed. The megafloral record does record a broader sampling of landscape diversity: only two of the five Markley facies-associated megafloral assemblage types per Tabor et al. (2013) are represented in the palynofloral record at Lycopod B (Lithofacies 2 and 3). In addition to dryland and wetland megafloral assemblages at Lycopod B East, Lycopod B West records another kaolinite unit containing walchian conifers above a wetland muck soil, much like the basal kaolinite unit at Lycopod B East. Another megafloral assemblage occurs at the base of the cap sandstone at Lycopod B West, unusual for its abundance of cordaitalean leaves, as well as rare medullosans and tree ferns. It presumably represents Lithofacies 5

(channel sandstone facies), and probably reflects typical elements of riparian vegetation, given its position at the base of a channel.

6.4 Sedimentary cycles and time in the Markley Formation

The Markley Formation lacks the marine fossils or volcanic ashes that would allow biostratigraphic or chronometric correlation with marine cyclothem exposed along the coastal margins of Pangaea. Nevertheless, sedimentation in this formation progresses in a repeating and predictable cycle, suggesting a correlation with glacioeustatic sea level and climate change linked to glacial/interglacial cycles. Critical to this inference is determining how much time is represented by a single sedimentary package (paleosol to cap sandstone, Fig. 1). Without firm chronometric or stratigraphic controls, time estimates based on sedimentary rates are imprecise, at best. The basal conifer bearing kaolinitic siltstone was probably deposited as a single, rapid sedimentation event from a flood event. There does not appear to have been a significant lag between deposition of the kaolinite and initiation of peat accumulation. By analogy with measurements of accumulation in recent peats on Papua New Guinea, one to several thousand years may separate these two beds, at most (Staub and Gastaldo, 2003). Rates of peat accumulation are quite variable, but under tropical conditions peats can accumulate up to 20 mm/year (Page et al., 2006). Given a compression factor of 5:1 (based on the significant fractions of mineral matter in these peats), a 20 cm thick coal, such as the ones at Lycopod B, could represent as little as 100 years. Realistically, most Markley coals represent a complex interplay of intermittent decay, accumulation and auto-compression prior to burial. Thus, the minimum rate is almost certainly a significant underestimate of the actual time represented by these thin peats; a more plausible estimate for their formation is several thousands of years. The approximately two meters of organic mudstones exposed at Lycopod B East show evidence of pedogenesis but retain some evidence of bedding planes and recognizable plant fragments, so are clearly immature. These units probably accumulated over hundreds or thousands of years. Although there are no obvious unconformities, numerous short hiatuses undoubtedly exist within this interval. Overall, the roughly 3.4 m of organic-rich sediments exposed at Lycopod B East could represent accumulation of as little as a few thousand years, to as much as several tens of thousands of years. Estimating the accumulation rate of the floodplain deposits above the organic beds exposed at Lycopod B West poses even more challenges, since they include a variety of paleosols and small channels encompassing diastems of unknown length. A reasonable assumption of an average deposition rate of 100 mm/ky yields an estimate of approximately 20,000 years for the two meters of heterolithic beds exposed Lycopod B West. Thus, Lycopod B, from kaolinite to cap sandstone, could represent as little as 25,000 to as much as 40,000 to 100,000 years. The longer estimate seems more likely, given the significant gaps represented by paleosols, and agrees with estimates of 800,000 to 1,000,000 years for the entire Markley Formation (DiMichele et al. 2005a).

These estimates represent time scales (10^5 years) congruent with glacial/interglacial periodicity as a driver of repetitive sedimentary patterns in the Markley Formation. Other possible explanations, such as tectonic movement or base level changes, operate at longer time scales and do not exhibit the same level of periodicity. Furthermore, the Midland Basin appears to have been tectonically inactive during deposition of the Markley Formation

(Hentz, 1988). Basin subsidence and accommodation appears to have been nearly constant during this time as well, again indicating that base level changes were not responsible for shifts in sedimentation patterns (Tabor et al., 2013). Where the boundary between glacial and interglacial lies in the Markley Formation depends on the preferred atmospheric circulation model. If higher rainfall and/or low seasonality is supposed to occur during glacial maxima, the initiation of organic deposition marks the beginning of the glacial cycle, and glacial minimum is marked by the onset of evidence of greater seasonality, either at the beginning of the heterolithic beds or with the formation of paleosols and channel sandstones. Alternatively, if glacial minima were correlated with higher rainfall patterns and/or lower seasonality, they would be marked by initiation of organic facies. At present, there is insufficient evidence to determine exactly where glacial cycles end or interglacials begin in the Markley Formation.

6.5 Do autocyclic or allocyclic processes account for floral shifts at Lycopod B?

The question remains: were wetland and dryland floras separated temporally or spatially? Invoking strictly autocyclic processes, the sedimentary sequence at Lycopod B can be interpreted as normal fluvial landscape evolution from backswamp to floodplain to active channel. Under this model, dryland plants (conifers, peltasperms, and others, many unknown) occupied driest parts of the landscape, such as elevated interfluves, while cordaitaleans, sphenopsids and some seed ferns occupied stream banks and wetter sites within the flood plain, and wetland plants such as ferns, lycopsids and seed ferns occupied sites with the highest water table and poor drainage. Interpretation of kaolinite units as aquicludes suggests that organic facies formed independently of climate. Palynological patterns can be similarly interpreted. For example, the mixed dryland/wetland assemblage at the top of the kaolinite could be interpreted as an ecotone between the two communities. Furthermore, the presence of low levels (<1%) of dryland taxa in wetlands (organic facies) indicates that their source may have been nearby. Long-distance transport of dryland taxa, although possible, is considered less likely because of low clastic input into the organic facies, indicating that most of the pollen and spores were locally derived from vegetation growing in or very close to the wetland. Especially if the wetlands at Lycopod B were dominated largely by species of Marattiales, which are believed to have formed closed canopy forests (DiMichele, 2014), little pollen from plants growing more distally would be likely to penetrate by means of pollen rain.

The complex sedimentary patterns observed at Lycopod B, and the apparent cyclicality of sedimentation throughout the Markley, both seem difficult to explain through autocyclic processes alone. Allocyclic processes, especially changes in precipitation and seasonality, are considered more likely responsible for these observed changes. Under this model, climate controls both sedimentary patterns and distribution of vegetation. Wetland and dryland taxa are predicted to succeed one another temporally but rarely coexist; they would normally be spatially separated, perhaps by hundreds of kilometers. Kaolinites might indeed form aquicludes, but that is alone is insufficient for peat formation: in addition, rainfall must exceed evapotranspiration for most of the year. Absence of peat or carbonaceous shales above the kaolinite unit at Lycopod B West, and several other localities, indicates that climate may have been too dry to allow peat formation at those times. The mixed

study of exceptional floral assemblages, where dryland and wetland assemblages are laterally juxtaposed, and precisely correlated to marine sequences, as the key to understanding how vegetation was distributed across the landscape in the Late Pennsylvanian.

Acknowledgments

We acknowledge William A. DiMichele for his generous sharing of samples and field notes, helpful discussions and support for this work. Ivo Duijnste and Robert Stevenson assisted with imaging, figure and plate preparation. Critiques by Henk Visscher, Tom van Hoof and especially Hans Kerp greatly improved the manuscript. Cindy Looy was supported by the Hellman Family Foundation. The research of Carol Hotton was supported in part by the Intramural Research Program of the National Institutes of Health, National Library of Medicine. This is ETE publication 337, and UCMF Contribution 2055.

References

- Allen JP, Fielding CR, Gibling MR, Rygel MC. Fluvial response to paleoequatorial climate fluctuations during the late Paleozoic ice age. *Geological Society of America Bulletin*. 2011; 123:1524–1538.
- Anderson, JM.; Anderson, HM. Palaeoflora of southern Africa, Molteno Formation (Triassic) 1. (Part 1. Introduction; Part 2. Dicroidium). Balkema; Rotterdam: 1983.
- Andrews HN, Agashe SN. A new sporangium from the American Carboniferous. *Palaeobotanist*. 1962; 11:46–48.
- Archer, AW. Cyclic sedimentation (cyclothem). In: Gornitz, V., editor. *Encyclopedia of paleoclimatology and ancient environments*. Springer; Dordrecht: 2009. p. 226–228.
- Ash SR, Litwin RJ. New species of the pinnate microsporophyll *Pramelreuthia* from the Upper Triassic of the southwestern United States. *American Journal of Botany*. 1996; 83:1091–1099.
- Balme BE. Fossil in situ spores and pollen grains: an annotated catalogue. *Review of Palaeobotany and Palynology*. 1995; 87:81–323.
- Bashforth AR, Falcon-Lang HJ, Gibling MR. Vegetation heterogeneity on a Late Pennsylvanian braided-river plain draining the Variscan Mountains, La Magdalena Coalfield, northwestern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 2010; 292:367–390.
- Bashforth A, Drábková J, Opluštil S, Gibling MR, Falcon-Lang HJ. Landscape gradients and patchiness in riparian vegetation on a Middle Pennsylvanian braided-river plain prone to flood disturbance (Nany Member, Central and Western Bohemian Basin, Czech Republic). *Review of Palaeobotany and Palynology*. 2011; 163:153–189.
- Bashforth AR, Cleal CJ, Gibling MR, Falcon-Lang HJ, Miller RF. Paleocology of Early Pennsylvanian vegetation on a seasonally dry tropical landscape (Tynemouth Creek Formation, New Brunswick, Canada). *Review of Palaeobotany and Palynology*. 2014; 200:229–263.
- Baxter RW. *Carinostrobis foresmani*, a new lycopod genus from the Middle Pennsylvanian of Kansas. *Palaeontographica Abteilung B*. 1971; 134:124–130.
- Beerbower JR. Cyclothem and cyclic depositional mechanisms in alluvial plain sedimentation. *Kansas Geological Survey Bulletin*. 1964; 169:31–42.
- Begon, M.; Townsend, CR.; Harper, JL. *Ecology from individuals to ecosystems*. 4. Blackwell Publishing; Oxford: 2006.
- Bek J, Pšenička J. *Senftenbergia plumosa* (Artis) emend., and its spores from the Carboniferous of the Kladno and Pilsen basins, Bohemian Massif, and some related and synonymous taxa. *Review of Palaeobotany and Palynology*. 2001; 116:213–232.
- Bek J, Drábková D, Daškov J, Libertín M. The sub-arborescent lycopsid genus *Polysporia* Newberry and its spores from the Pennsylvanian (Bolsovian–Stephanian B) continental basins of the Czech Republic. *Review of Palaeobotany and Palynology*. 2008; 152:176–199.
- Bek J, Libertín M. *In situ* reticulate sphenophyllalean spores, Pennsylvanian (Bolsovian) of the Czech Republic. *Review of Palaeobotany and Palynology*. 2010; 159:56–61.

- Birgenheier LP, Fielding CR, Rygel MC, Frank TD, Roberts J. Evidence for dynamic climate change on sub-10⁶-year scales from the late Paleozoic glacial record, Tamworth Belt, New SouthWales, Australia. *Journal of Sedimentary Research*. 2009; 79:56–82.
- Boyce CK, Abrecht M, Zhou D, Gilbert PUPA. X-ray photoelectron emission spectromicroscopic analysis of arborescent lycopoid cell wall composition and Carboniferous coal ball preservation. *International Journal of Coal Geology*. 2010; 83:146–153.
- Brousmitche C. Les fougères sphenopteridiennes du bassin houiller sarro-lorrain (Systematique-Stratigraphie). *Annales de la Société géologique du Nord*. 1983; 10:1–480.
- Brousmitche C. Précisions sur les spores produites par quelques sphenopteridiennes appartenant aux genres *Boweria* Kidston, *Crossotheca* Zeiller, *Discopteris* Stur, *Myriotheca* Zeiller et *Urnatopteris* Kidston. *Revue de Paléobiologie*. 1986; 5:231–248.
- Brousmitche-Delcambre C, Lugardon B, Coquel R, Goubet P. Découverte dans le bassin houiller sarro-lorrain du genre *Radiitheca* (organes reproducteurs de Filicophytes) et ultrastructure du genre *Microreticulatisporites*. *Geobios*. 1997; 30:3–14.
- Bunting MJ. Pollen in wetlands: using simulations of pollen dispersal and deposition to better interpret the pollen signal. *Biodiversity and Conservation*. 2008; 17:2079–2096.
- Burnham RJ. Reconstructing richness in the plant fossil record. *Palaeos*. 1993; 8:376–384.
- Cecil, CB.; Dulong, FT. Precipitation models for sediment supply in warm climates. In: Cecil, CB.; Edgar, TN., editors. *Climate controls on stratigraphy*. 2003. p. 21-27. *SEPM Special Publication 77*
- Cecil, CB.; Dulong, FT.; West, RR.; Stamm, R.; Wardlaw, B.; Edgar, NT. Climate controls on the stratigraphy of a Middle Pennsylvanian cyclothem in North America. In: Cecil, CB.; Edgar, TN., editors. *Climate controls on stratigraphy*. 2003. p. 151-182. *SEPM Special Publication 77*
- Cecil CB, DiMichele WA, Elrick SD. Middle and Late Pennsylvanian cyclothem, American Midcontinent: Ice-age environmental changes and terrestrial biotic dynamics. *Comptes Rendus Geoscience*. 2014; 346:159–168.
- Chaloner WG. The Carboniferous upland flora. *Geological Magazine*. 1958a; 95:261–262.
- Chaloner WG. *Polysporia mirabilis* Newberry, a fossil lycopod cone. *Journal of Palaeontology*. 1958b; 32:199–209.
- Chaphekar M, Alvin KL. On the fertile parts of the coenopterid fern *Metaclepsydropsis duplex* (Williamson). *Review of Palaeobotany and Palynology*. 1972; 14:63–76.
- Clement-Westerhof JA. Aspects of Permian palaeobotany and palynology. IV. The conifer *Ortiseia* Florin from the Val Gardena Formation of the Dolomites and Vicentinian Alps (Italy) with special reference to a revised concept of the Walchiaceae (Göppert) Schimper. *Review of Palaeobotany and Palynology*. 1984; 41:51–166.
- Cridland AA, Morris JE. *Taeniopteris*, *Walchia*, and *Dichophyllum* in the Pennsylvanian system in Kansas. *University of Kansas Science Bulletin*. 1963; 44:71–85.
- Dickey BC, Gupta S. Palynostratigraphy of the Newcastle Coal of north central Texas, U.S.A. *Pollen et Spores*. 1980; 22:545–553.
- DiMichele WA, Phillips TL. Paleobotanical and paleoecological constraints on models of peat formation in the Late Carboniferous of Euramerica, *Palaeogeography, Palaeoclimatology, Palaeoecology*. 1994; 106:39–90.
- DiMichele WA, Phillips TL. Climate change, plant extinctions, and vegetational recovery during the Middle-Late Pennsylvanian transition: the case of tropical peat-forming environments in North America. *Geological Society Special Publication*. 1996; 102:201–221.
- DiMichele WA, Chaney DS, Dixon WH, Nelson WJ, Hook RW. An Early Permian coastal flora from the Central Basin Platform of Gaines County, West Texas. *Palaeos*. 2000; 15:524–534.
- DiMichele WA, Mamay SH, Chaney DS, Hook RW. An Early Permian flora with Late Permian and Mesozoic affinities from North-Central Texas. *Journal of Paleontology*. 2001; 75:449–460.
- DiMichele WA, Hook RW, Nelson WJ, Chaney DS. An unusual middle Permian flora from the Blaine Formation (Pease River Group, Leonardian-Guadalupian Series) of King County, West Texas. *Journal of Paleontology*. 2004; 78:765–782.
- DiMichele, WA.; Kerp, H.; Krings, M.; Chaney, DS. The Permian peltasperm radiation: evidence from the southwestern United States. In: Lucas, SG.; Zeigler, KE., editors. *The nonmarine Permian*. Vol. 30. 2005b. p. 67-79. *New Mexico Museum of Natural History and Science Bulletin*

- DiMichele, WA.; Tabor, NJ.; Chaney, DS. Outcrop-scale environmental heterogeneity and vegetational complexity in the Permo-Carboniferous Markley Formation of north-central Texas. In: Lucas, SG.; Zeigler, KE., editors. *The Nonmarine Permian*. Vol. 30. 2005a. p. 60-66. New Mexico Museum of Natural History and Science Bulletin
- DiMichele, WA.; Tabor, NJ.; Chaney, DS.; Nelson, WJ. From wetlands to wet spots: environmental tracking and the fate of Carboniferous elements in Early Permian tropical floras. In: Greb, SF.; DiMichele, WA., editors. *Wetlands through time*. Vol. 399. 2006. p. 223-248. Geological Society of America Special Paper
- DiMichele WA, Montañez IP, Poulsen CJ, Tabor NJ. Climate and vegetational regime shifts in the late Paleozoic ice age earth. *Geobiology*. 2009; 7:200–226. [PubMed: 19320746]
- DiMichele WA, Cecil CB, Montañez IP, Falcon-Lang HJ. Cyclic changes in Pennsylvanian paleoclimate and effects on floristic dynamics in tropical Pangaea. *International Journal of Coal Geology*. 2010; 83:329–344.
- DiMichele WA, Falcon-Lang HJ. Pennsylvanian ‘fossil forests’ in growth position (T⁰ assemblages): origin, taphonomic bias and palaeoecological insights. *Journal of the Geological Society, London*. 2011; 168:585–605.
- DiMichele WA, Kerp H, Sirmons R, Fedorko N, Skema V, Blake BM Jr, Cecil CB. Callipterid peltasperms of the Dunkard Group, Central Appalachian Basin. *International Journal of Coal Geology*. 2013; 119:56–78.
- DiMichele WA. Wetland-dryland vegetational dynamics in the Pennsylvanian ice age tropics. *International Journal of Plant Science*. 2014; 175:123–164.
- Dimitrova T, Cleal CJ, Thomas BA. Palynological evidence for Pennsylvanian extra-basinal vegetation in Atlantic Canada. *Journal of the Geological Society, London*. 2011; 168:559–569.
- Dolby G, Falcon-Lang HJ, Gibling M. A conifer-dominated palynological assemblage from Pennsylvanian (late Moscovian) alluvial drylands in Atlantic Canada: implications for the vegetation of tropical lowlands during glacial phases. *Journal of the Geological Society, London*. 2011; 168:571–584.
- Doubinger J, Grauvogel-Stamm L. Présence de spores du genre *Thymospora* chez *Pecopteris hemiteliodes* du Mont-Pélé (Stephanian moyen du Bassin d’Autun). *Pollen et Spores*. 1971; 12:598–607.
- Eble, CF.; Blake, BM.; Gillespie, WH.; Pfefferkorn, HW. Appalachian basin fossil floras. In: Greb, SF.; Chesnut, D., editors. *Carboniferous of the Appalachian and Black Warrior Basins*. Vol. 10. 2009. p. 46-58. Kentucky Geological Survey Special Publication
- Eggert DA, Delevoryas T. Studies of Paleozoic ferns: *Sermeya*, gen. nov. and its bearing on filicalean evolution in the Paleozoic. *Palaeontographica Abteilung B*. 1967; 118:169–180.
- Eros JM, Montañez IP, Osleger DA, Davydov VI, Nemyrovska TI, Poletaev VI, Zhykalyak MV. Sequence stratigraphy and onlap history of the Donets Basin, Ukraine: insight into Carboniferous icehouse dynamics. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 2012; 313–314:1–25.
- Falcon-Lang HJ. Pennsylvanian tropical rain forests responded to glacial-interglacial rhythms. *Geology*. 2004; 32:689–692.
- Falcon-Lang HJ, Bashforth AR. Morphology, anatomy, and upland ecology of large cordaitalean trees from the Middle Pennsylvanian of Newfoundland. *Review of Palaeobotany and Palynology*. 2005; 135:223–243.
- Falcon-Lang HJ, Jud NA, Nelson WJ, DiMichele WA, Chaney DS, Lucas SG. Pennsylvanian coniferopsid forests in sabkha facies reveal the nature of seasonal tropical biomes. *Geology*. 2011a; 39:371–374.
- Falcon-Lang HJ, Pendleton JL. Dryland plant communities in the Pennsylvanian (mid- to late Bolsovian) Winterbourne Formation of Bristol, southern Britain: Further evidence for taphonomic megabias. *Review of Palaeobotany and Palynology*. 2011b; 166:268–285.
- Feldman HR, Franseen EK, Joeckel RM, Heckel PH. Impact of longer-term modest climate shifts on architecture of high-frequency sequences (cyclothems), Pennsylvanian of Midcontinent USA. *Journal of Sedimentary Research*. 2005; 75:350–368.

- Fielding CR, Frank TD, Isbell JL. The late Paleozoic ice age—A review of current understanding and synthesis of global climate patterns. *Geological Society of America Special Papers*. 2008; 441:343–354.
- Florin R. Die Koniferen des Oberkarbons und des Unteren Perms. *Palaeontographica Abteilung B*. 1944; 85:365–456.
- Galtier J, Taylor TN. The first record of ferns from the Permian of Antarctica. *Review of Palaeobotany and Palynology*. 1994; 83:227–239.
- Gastaldo RA, Stevanovic-Walls IM, Ware WN, Greb SF. Community heterogeneity of Early Pennsylvanian peat mires. *Geology*. 2004; 32:693–696.
- Gastaldo RA. Peat or no peat: Why do the Rajang and Mahakam Deltas differ? *International Journal of Coal Geology*. 2010; 83:162–172.
- Gastaldo, RA.; Demko, TM. Long term hydrology controls the plant fossil record. Taphonomy: processes and bias through time. In: Allison, PA.; Bottjer, DJ., editors. *Topics in Geobiology*. 2. Vol. 32. 2011. p. 249-286.
- Gardner, TW.; Williams, EG.; Holbrook, PW. Pedogenesis of some Pennsylvanian underclays: ground-water, topographic and tectonic controls. In: Reinhardt, J.; Sigleo, WR., editors. *Paleosols and weathering through geological time: principles and applications*. Vol. 216. 1988. p. 81-102. *Geological Society of America Special Paper*
- Gomankov AV, Meyen SV. Tatarian flora (composition and distribution in the Late Permian of Eurasia). *Transactions of Geological Institute of Academy of Sciences USSR*. 1986; 401:1–173. (in Russian).
- Good CW. A petrified fern sporangium from the British Carboniferous. *Palaeontology*. 1981; 24:483–492.
- Gould RE, Delevoryas T. The biology of *Glossopteris*: evidence from petrified seed-bearing and pollen-bearing organs. *Alcheringia*. 1977; 1:387–399.
- Grauvogel-Stamm L, Doubinger J. Deux fougères fertiles du Stéphaniens du Massif Central (France). *Geobios*. 1975; 6:409–421.
- Grauvogel-Stamm L. La flore du Grès à Voltzia (Buntsandstein supérieur) des Vosges du Nord (France). Morphologie, anatomie, interprétations phylogénique et paléogéographique. *Université Louis-Pasteur de Strasbourg Institut de Géologie*. 1978; 50:1–225.
- Grauvogel-Stamm L, Grauvogel L. *Masculostrobus acuminatus* nom. nov., un nouvel organe reproducteur mâle de Gymnosperme de Grès à Voltzia (Trias inférieur) des Vosges (France). *Geobios*. 1973; 6:101–114.
- Hammer Ø, Harper DAT, Ryan PD. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*. 2001; 4:1–9.
- Heckel, PH. Pennsylvanian cyclothem in Midcontinent North America as far-field effects of waxing and waning of Gondwana ice sheets. In: Fielding, CR.; Frank, TD.; Isbell, JL., editors. *Resolving the Late Paleozoic Ice Age in time and space*. Vol. 441. 2008. p. 275-289. *Geological Society of America Special Paper*
- Hemsley, AR. Exine ultrastructure in the spores of enigmatic Devonian plants: its bearing on the interpretation of relationships and on the origin of the sporophyte. In: Kurmann, MH.; Doyle, JA., editors. *Ultrastructure of fossil spores and pollen*. The Royal Botanic Gardens; Kew, London: 1994. p. 1-21.
- Hentz TF. Lithostratigraphy and paleoenvironments of Upper Paleozoic continental red beds, north-central-central Texas: Bowie (new) and Wichita (revised) Groups. *Bureau of Economic Geology Report of Investigations*. 1988; 170:1–55.
- Hernandez-Castillo GR, Rothwell GW, Mapes G. Thucydiaceae fam. nov., with a review and reevaluation of Paleozoic waldian conifers. *International Journal of Plant Science*. 2001; 162:1155–1185.
- Hilton J, Bateman RM. Pteridosperms are the backbone of seed-plant phylogeny. *Journal of the Torrey Botanical Society*. 2006; 133:119–168.
- Holden HS. The morphology of *Botryopteris antiqua* Kidston. *Br Mus Nat Hist Bull*. 1962; 5:361–380.
- Horton DE, Poulsen CJ, Pollard D. Influence of high-latitude vegetation feedbacks on late Palaeozoic glacial cycles. *Nature Geoscience*. 2010; 3:572–577.

- Horton DE, Poulsen CJ, Montañez IP, DiMichele WA. Eccentricity-paced late Paleozoic climate change. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 2012; 331–332:150–161.
- Hupp CR, Osterkamp WR. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. *Ecology*. 1985; 66:670–681.
- Kerp JHF. Aspects of Permian palaeobotany and palynology. X. The Western and Central European species of the genus *Autunia* Krasser emend. Kerp (Peltaspermaeae) and the form genus *Rhachiphyllum* Kerp (callipterid foliage). *Review of Palaeobotany and Palynology*. 1988; 54:249–360.
- Kerp H. Post-Variscan Late Palaeozoic Northern Hemisphere gymnosperms: the onset to the Mesozoic. *Review of Palaeobotany and Palynology*. 1996; 90:263–285.
- Kerp, H. The modernization of landscapes during the Late Paleozoic-Early Mesozoic. In: Gastaldo, RA.; DiMichele, WA., editors. *Phanerozoic terrestrial ecosystems*. Vol. 6. 2000. p. 79–113. *Paleontological Society Papers*
- Krassilov VA, Afonin SA, Naugolnykh SV. *Permothecca* with *in situ* pollen grains from the Lower Permian of the Urals. *Palaeobotanist*. 1999; 48:19–25.
- Labandeira, CC. The paleobiology of pollination and its precursors. In: Gastaldo, RA.; DiMichele, WA., editors. *Phanerozoic terrestrial ecosystems*, *Paleontological Society Papers*. Vol. 6. 2000. p. 233–269.
- Lesnikowska, AD. Dissertation. University of Illinois; Urbana-Champaign: 1989. Anatomically preserved Marattiales from coal swamps of the Desmoinesian and Missourian of the Midcontinent United States: systematics, ecology and evolution; p. 1–227.
- Lesnikowska AD, Willard DA. Two new species of *Scoleopteris* (Marattiales), sources of *Torispora securis* Balme and *Thymospora thiessenii* (Kosanke) Wilson et Venkatachala. *Review of Palaeobotany and Palynology*. 1997; 95:211–225.
- Libertín M, Bek J, Drábková J. Two new Carboniferous fertile sphenophylls and their spores from the Czech Republic. *Acta Palaeontologica Polonica*. 2008; 53:723–732.
- Libertín M, Bek J, Drábková J. New sphenophyllaleans from the Pennsylvanian of the Czech Republic. *Review of Palaeobotany and Palynology*. 2014; 200:196–210.
- Lindström S, McLoughlin S, Drinnan AN. Intraspecific variation of taeniate bisaccate pollen within Permian glossopterid sporangia, from the Prince Charles Mountains, Antarctica. *International Journal of Plant Sciences*. 1997; 158:673–684.
- Looy CV. Extending the range of derived Late Paleozoic conifers: *Lebowskia* gen. nov. (Majonicaceae). *International Journal of Plant Sciences*. 2007; 168:957–972.
- Looy CV. Natural history of a plant trait: branch system abscission in Paleozoic conifers and its environmental, autecological and ecosystem implications. *Paleobiology*. 2013; 39:235–252.
- Looy, CV.; Duijnste, IAP. Characterizing morphologic variability in foliated Paleozoic conifer branches – a first step in testing its potential as proxy for taxonomic position. In: Lucas, SG.; DiMichele, WA.; Barrick, JE.; Schneider, JW.; Spielmann, JA., editors. *The Carboniferous-Permian transition*. Vol. 60. 2013. p. 215–223. *New Mexico Museum of Natural History and Science Bulletin Series*
- Looy CV, Stevenson RA. Earliest occurrence of autorotating seeds in conifers: the Permian (Kungurian-Roadian) *Manifera talaris* gen. et sp. nov. *International Journal of Plant Sciences*. 2014; 175:841–854.
- Lyons PC, Darrah WC. Earliest conifers of North America: Upland and/or paleoclimatic indicators? *Palaios*. 1989; 4:480–486.
- Mamay SH, Miller JM, Rohr DR, Stein WE Jr. Foliar morphology and anatomy of the gigantopterid plant *Delnortea abbottiae*, from the Lower Permian of West Texas. *American Journal of Botany*. 1988; 75:1409–1433.
- Mapes, G.; Rothwell, GW. Diversity among Hamilton conifers. In: Mapes, G.; Mapes, RH., editors. *Regional geology and paleontology of Upper Paleozoic Hamilton quarry area in southeastern Kansas*. Vol. 6. 1988. p. 225–244. *Kansas Geological Survey Guidebook Series*
- Meyen SV. Basic features of gymnosperm systematics and phylogeny as shown in the fossil record. *Botanical Reviews*. 1984; 50:1–111.

- Meyen SV. Permian conifers of western Anagaraland. Review of Palaeobotany and Palynology. 1997; 96:351–447.
- Millay MA. *Acaulangium* gen. n., a fertile marattialean from the Upper Pennsylvanian of Illinois. Amer J Bot. 1977; 64:223–229.
- Millay MA. Studies of Paleozoic Marattialeans: A monograph of the American species of *Scolecoperis*. Palaeontographica Abteilung B. 1979; 169:1–69.
- Millay MA, Taylor TN. Paleozoic seed fern pollen organs. Bot Rev. 1979; 45:301–375.
- Millay MA, Taylor TN. The ultrastructure of Paleozoic fern spores: I. *Botryopteris*. American Journal of Botany. 1982; 69:1148–1155.
- Millay MA, Taylor TN. The ultrastructure of Paleozoic fern spores. II. *Scolecoperis* (Marattiales). Palaeontographica Abteilung B. 1984; 194:1–13.
- Montañez IP, Tabor NJ, Niemeier D, DiMichele WA, Frank TD, Fielding CR, Isbell JL, Birgenheier LT, Rygel M. CO₂-forced climate and vegetation instability during Late Paleozoic glaciation. Science. 2007; 315:87–91. [PubMed: 17204648]
- Montañez IP, Poulsen CJ. The Late Paleozoic Ice Age: an evolving paradigm. Annual Reviews in Earth and Planetary Science. 2013; 41:629–656.
- Naugolnykh SV. New male reproductive organs of gymnosperms *Permotheca colovratika* sp. nov. from the Lower Permian of the Ural Mountains. Paleontological Journal. 2013; 47:114–126.
- Neves R, Gueinn KJ, Clayton G, Ioannides NS, Kruszewska K. Palynological correlations within the Lower Carboniferous of Scotland and Northern England. Transactions of the Royal Society of Edinburgh. 1973; 69:23–76.
- Nichols DJ. Palynology in the coal systems analysis - the key to floras, climate, and stratigraphy of coal forming environments. Geological Society of America Special Papers. 2005; 387:51–58.
- Opluštil S, Bek J. Some Pennsylvanian arborescent lycopsid cones and their microspores from the British coalfields. Bulletin of Geosciences. 2009; 84:203–226.
- Opluštil S, Bek J, Drábková J. A new bisporangiate lycopsid cone genus *Thomasostrobus* gen. nov. from the Late Pennsylvanian of the Intra-Sudetic Basin (Czech Republic). Bulletin of Geosciences. 2009; 84:283–300.
- Osborn JM, Taylor TN. Pollen morphology and ultrastructure of the Corytospermales: permineralized in situ grains from the Triassic of Antarctica. Review of Palaeobotany and Palynology. 1993; 79:205–219.
- Osterkamp WR, Hupp CR. Fluvial processes and vegetation - glimpses of the past, the present, and perhaps the future. Geomorphology. 2010; 116:274–285.
- Page, SE.; Rieley, JO.; Wuest, R. Lowland tropical peatlands of Southeast Asia. In: Martini, P.; Martínez Cortizas, A.; Chesworth, W., editors. Peatlands: evolution and records of environmental and climate changes. Elsevier; Amsterdam: 2006. p. 145-172.
- Peppers RA. Palynological correlation of major Pennsylvanian (Middle and Upper Carboniferous) chronostratigraphic boundaries in the Illinois and other coal basins. Geological Society of America Memoirs. 1996; 188:1–112.
- Peyser CE, Poulsen CJ. Controls on Permo-Carboniferous precipitation over tropical Pangaea: a GCM sensitivity study. Palaeogeography, Palaeoclimatology, Palaeoecology. 2008; 268:181–192.
- Pfefferkorn HW, Peppers RA, Phillips TL. Some fern-like fructifications and their spores from the Mazon Creek compression flora of Illinois (Pennsylvanian). Illinois State Geological Survey, Circular. 1971; 463:1–54.
- Pfefferkorn HW. A note on the term “upland”flora. Review of Palaeobotany and Palynology. 1980; 30:157–158.
- Playford G, Dino R. Palynostratigraphy of upper Palaeozoic strata (Tapajós Group), Amazonas Basin, Brazil: part one. Palaeontographica Abteilung B. 2000; 255:1–46.
- Plotnick RE, Kenig F, Scott AC, Glasspool IJ, Eble CF, Lang WJ. Pennsylvanian paleokarst and cave fills from northern Illinois, USA: a window into late Carboniferous environments and landscapes. Palaios. 2009; 24:627–637.
- Pointon MA, Chew DM, Ovtcharova M, Sevastopulo GD, Crowley QG. New high-precision U-Pb dates from western European Carboniferous tuffs; implications for timescale calibration, the

- periodicity of late Carboniferous cycles and stratigraphical correlation. *Journal of the Geological Society, London*. 2012; 169:713–721.
- Poort R, Clement-Westerhof JA, Looy CV, Visscher H. Conifer extinction in Europe at the Permian-Triassic junction: morphology, ultrastructure and geographic-stratigraphic distribution of *Nuskoisporites dulhuntyi* (prepollen of *Ortiseia*, Walchiaceae). *Review of Palaeobotany and Palynology*. 1997; 97:9–39.
- Potonié R. Synopsis der Sporae *in situ*. Beihefte zum Geologischen Jahrbuch. 1962; 52:1–204.
- Potonié R. Versuch der Einordnung der fossilen Sporae dispersae in das phylogenetische System der Pflanzenfamilien. I. Thallophyta bis Gnetales. II. Angiospermae. *Forschungsberichte des Landes Nordrhein-Westfalen*. 1967; 1761:1–310.
- Pšeni ka J, Bek J, Zodrow EL, Cleal CJ, Hemsley A. A new late Westphalian fossil marattialean fern from Nova Scotia. *Botanical Journal of the Linnean Society*. 2003; 142:199–212.
- Pšeni ka J, Zodrow EL, Bek J. A reassessment of the taxonomy of *Oligocarpia bellii* (Late Pennsylvanian, Sydney Coalfield, Nova Scotia, Canada). *Palaeontographica, Abteilung B*. 2005; 272:51–65.
- Ravn RL. Palynostratigraphy of the Lower and Middle Pennsylvanian coals of Iowa. *Iowa Geological Survey Technical Paper*. 1986; 7:1–245.
- Rees PM, Ziegler AM, Gibbs MT, Kutzbach JE, Behrling PJ, Rowley DB. Permian phytogeographic patterns and climate data/model comparisons. *Journal of Geology*. 2002; 110:1–31.
- Remy W, Remy R. Durch Mazeration fertiler Farne des Paläozoikums gewonnene Sporen. *Paläontologische Zeitschrift*. 1957; 31:55–65.
- Remy W, Rettschlag R. Neue Untersuchungen über die Pollen von *Schuetzia anomala* H. B. Geinitz. *Geologie*. 1954; 3:582–589.
- Retallack GJ, Dilcher DL. Reconstructions of selected seed ferns. *Annals of the Missouri Botanical Garden*. 1988; 75:1010–1057.
- Riggs SD, Rothwell GW. *Sentistrobus goodii* n. gen. and sp., a permineralized sphenophyllalean cone from the Upper Pennsylvanian of the Appalachian Basin. *Journal of Paleontology*. 1985; 59:1194–1202.
- Rothwell GW. The Callistophytales (Pteridospermopsida): Reproductively sophisticated Palaeozoic gymnosperms. *Review of Palaeobotany and Palynology*. 1981; 32:103–121.
- Rothwell GW, Mapes G, Hernandez-Castillo GR. *Hanskerpia* gen. nov. and phylogenetic relationships among the most ancient conifers (Voltziales). *Taxon*. 2005; 54:733–750.
- Rueger BF. Palynology and its relationship to climatically induced depositional cycles in the Middle Pennsylvanian (Desmoinesian) Paradox Formation of southeastern Utah. *US Geological Survey Bulletin*. 1996; 2000-K:K1–K22.
- Schwendemann AB, Wang G, Mertz ML, McWilliams RT, Thatcher SL, Osborn JM. Aerodynamics of saccate pollen and its implications for wind pollination. *American Journal of Botany*. 2007; 94:1371–1381. [PubMed: 21636505]
- Scotese, C. PALEOMAP Project. Department of Geology, University of Texas; Arlington, TX: 1999. PALEOMAP Animations 'Paleogeography'.
- Srivastava SC. *Lelestrobis*: a new microsporangiata organ from the Triassic of Nidpur, India. *Palaeobotanist*. 1984; 32:86–90.
- Staub, JR.; Gastaldo, RA. Late Quaternary incised-valley fill and deltaic sediments in the Rajang River Delta. In: Sidi, HF.; Nummedal, D.; Imbert, P.; Darman, H.; Posamentier, HW., editors. *Tropical deltas of southeast Asia – sedimentology, stratigraphy, and petroleum geology*. Vol. 76. 2003. p. 71–87. SEPM Special Publication
- Tabor NJ. Permo-Pennsylvanian palaeotemperatures from Fe-Oxide and phyllosilicate $\delta^{18}\text{O}$ values. *Earth Planet Sci Lett*. 2007; 253:159–171.
- Tabor NJ, Montañez IP. Permo-Pennsylvanian alluvial paleosols (north-central Texas): High-resolution proxy records of the evolution of early Pangean paleoclimate. *Sedimentology*. 2004; 51:851–884.
- Tabor, NJ.; Montañez, IP.; Scotese, CR.; Poulsen, CJ.; Mack, GH. Paleosol archives of environmental and climatic history in paleotropical western Pangea during the latest Pennsylvanian through Early Permian. In: Fielding, CR.; Frank, TD.; Isbell, JL., editors. *Resolving the Late Paleozoic*

Ice Age in Time and Space. Vol. 441. 2008. p. 291-303. Geological Society of America Special Paper

- Tabor NJ, Poulsen CJ. Palaeoclimate across the Late Pennsylvanian–Early Permian tropical palaeolatitudes: A review of climate indicators, their distribution, and relation to palaeophysiographic climate factors. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 2008; 268:293–310.
- Tabor NJ, Romanchock CM, Looy CV, Hotton C, DiMichele WA, Chaney DS. Conservatism of Late Pennsylvanian vegetational patterns during short-term cyclic and long-term directional environmental change, western equatorial Pangaea. Geological Society, London, Special Publications. 2013; 376:201–234.
- Taylor TN. On the structure and phylogenetic relationships of the fern *Radstockia* Kidston. *Palaeontology*. 1967; 10:43–46.
- Taylor WA. Ultrastructural studies of sphenophyllalean spores. *Review of Paleobotany and Palynology*. 1986; 47:105–128.
- Taylor TN, Millay MA. Pollination biology and reproduction in early seed plants. *Review of Paleobotany and Palynology*. 1979; 27:329–355.
- Taylor TN, Rothwell GW. Studies of seed fern pollen: development of the exine in *Monoletes* (Medullosales). *American Journal of Botany*. 1982; 69:570–578.
- Taylor, TN.; Taylor, EL.; Krings, M. *Paleobotany: the biology and evolution of fossil plants*. Academic Press; Burlington, MA: 2009.
- Traverse, A. *Topics in Geobiology*. 2. Vol. 28. Springer; Dordrecht: 2007. *Paleopalynology*.
- Walling DE, He Q. The spatial variability of overbank sedimentation on river floodplains. *Geomorphology*. 1998; 24:209–223.
- Wanless HR, Shepard FP. Sea level and climatic changes related to late Paleozoic cycles. *Geological Society of America Bulletin*. 1936; 47:1177–1206.
- Wardlaw BR. Age assignment of the Pennsylvanian–Early Permian succession of North Central Texas. *Permophiles*. 2005; 46:21–22.
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ. Phylogenies and community ecology. *Annual Review of Ecology, Evolution, and Systematics*. 2002; 33:475–505.
- Wing SL, DiMichele WA. Conflict between local and global changes in plant diversity through geological time. *Palaios*. 1995; 10:551–564.
- Winston RB. A Late Pennsylvanian upland flora in Kansas: systematics and environmental implications. *Review of Palaeobotany and Palynology*. 1983; 40:5–31.
- Yao Z, Taylor TN. On a new gleicheniaceus fern from the Permian of South China. *Review of Palaeobotany and Palynology*. 1988; 54:121–134.
- Zavada MS. The ultrastructure of pollen found in dispersed sporangia of *Arberiella* (Glossopteridaceae). *Botanical Gazette*. 1991; 152:248–255.
- Zavialova N, Van Konijnenburg-van Cittert JHA. Exine ultrastructure of in situ peltasperm pollen from the Rhaetian of Germany and its implications. *Review of Palaeobotany and Palynology*. 2011; 168:7–20.
- Zodrow EL, Šimůnek Z, Cleal CJ, Bek J, Pšeni ka J. Taxonomic revision of the Palaeozoic marattialean fern *Acitheca* Schimper. *Review of Palaeobotany and Palynology*. 2006; 138:239–280.

Highlights

A palynological analysis from a latest Pennsylvanian locality from Texas is described

The LycopodB section represents one single interglacial/glacial phase

Plant communities are reconstructed using the palynomorphs' botanical affinities

Dryland and wetland floras succeed one another with little species turnover

Dryland and wetland assemblages are in close spatial proximity on the landscape

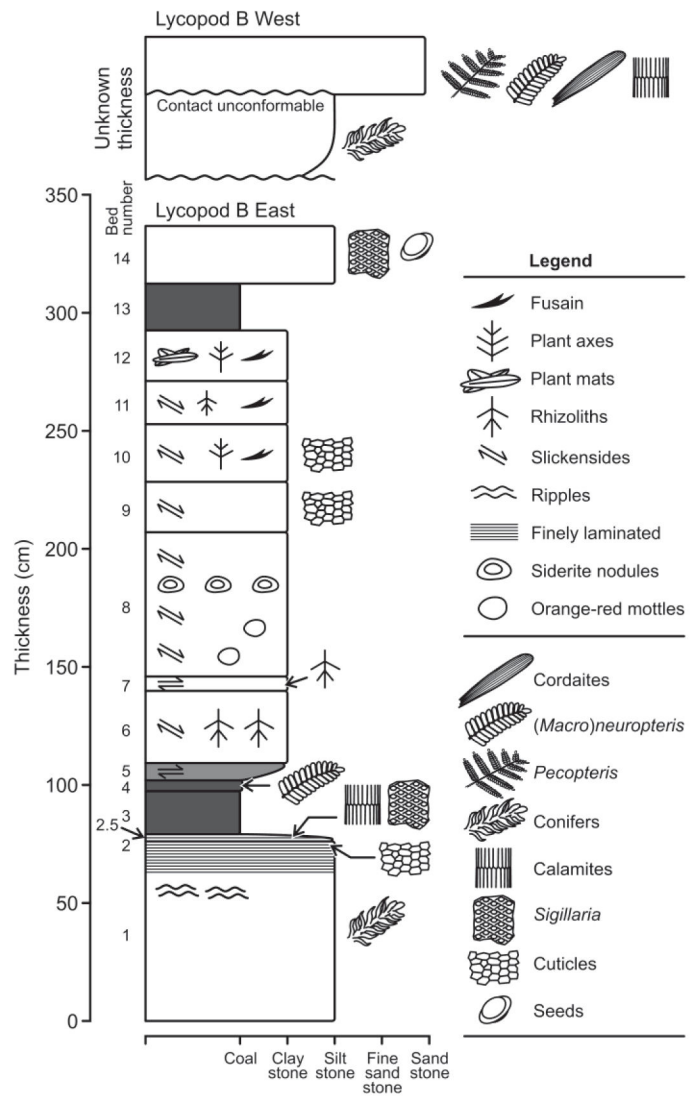


Fig. 1. Composite section of localities Lycopod B West and East, Markley Formation, north-central Texas.



Fig. 2. Lycopod B East locality outcrop (informal collection name 1990-31; USNM localities 40081, 40682, and 43546). Indicated are the bottom and top of the sampled and measured section. Numbers on the image indicate the lithologically distinct units, each sampled for palynological analysis, except for beds 5 and 11. The people are Ken Craddock (seated left), Christopher Durden (standing center) and Dan Chaney (right; DiMichele pers. comm. 2011).

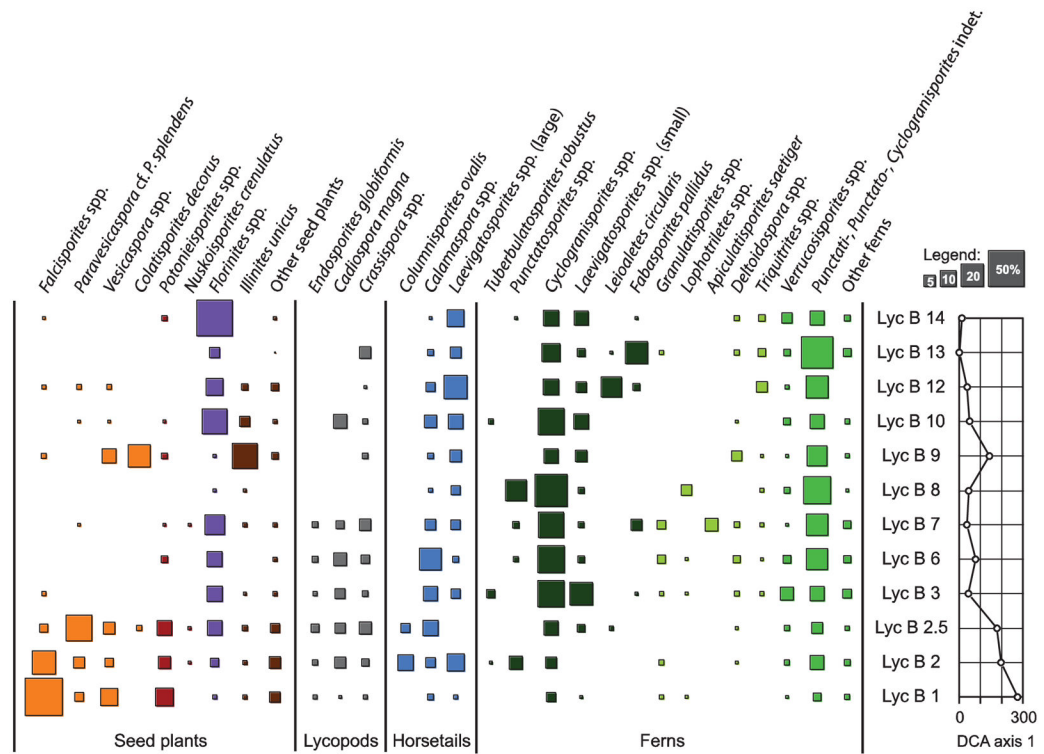


Fig. 3. Taxonomic composition and percent relative abundance of selected pollen and spore types per sample. Palynomorph taxa or groups of taxa are clustered according to their botanical affinity. The surface area of each square is a measure for a taxon’s relative abundance in a sample. As a summarizing measure for the dominant compositional changes along the section, the sample scores on the first axis of a DCA (see Fig. 5) are plotted on the right. Colors (from left to right): orange = seed ferns; red = conifers; purple = cordaitaleans; brown = other seed plants; grey = lycopods; blue = horsetails; dark green = tree ferns; light green = herbaceous ferns; intermediate green = other ferns.

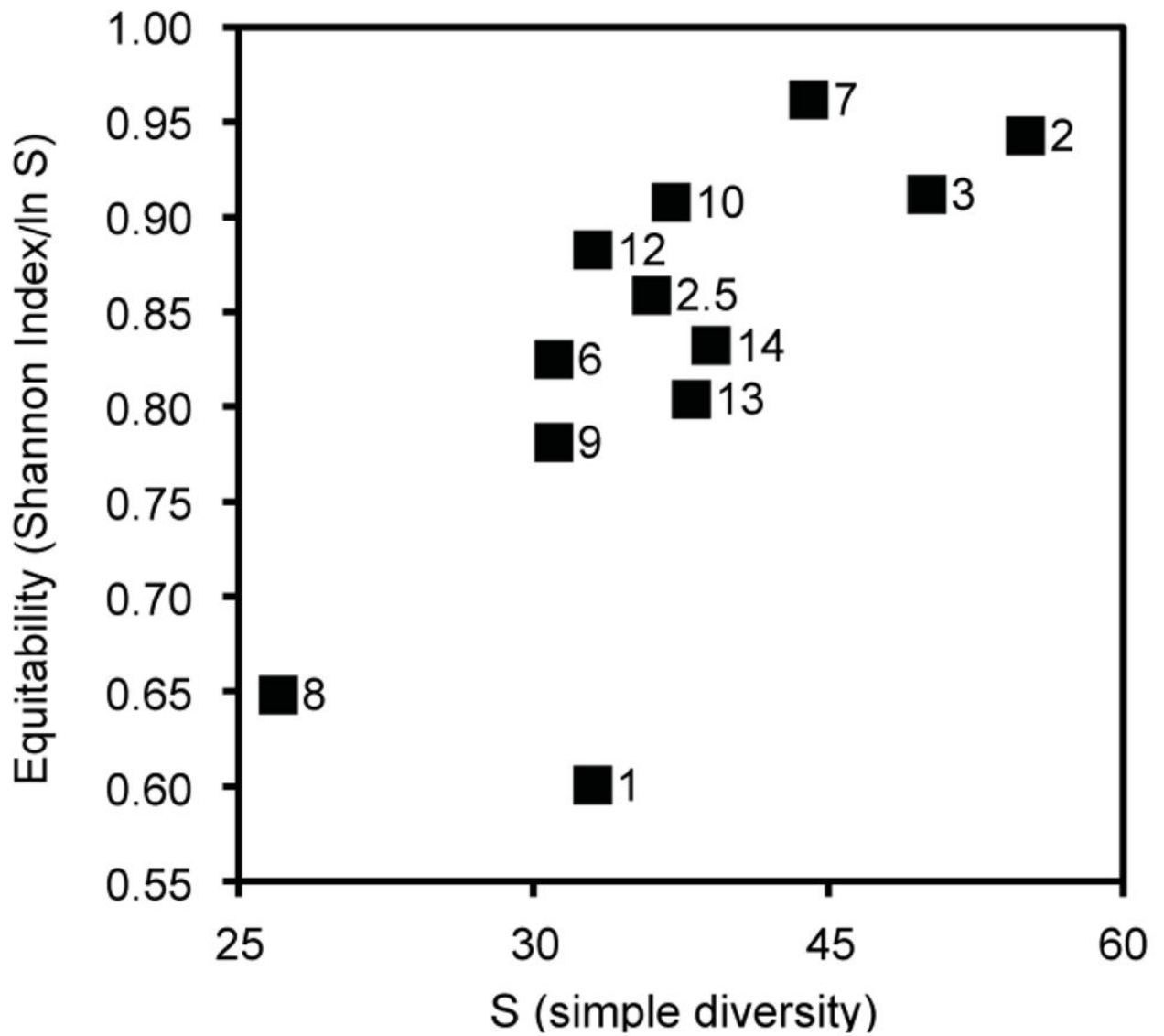


Fig. 4. Diversity aspects of palynological samples. Equitability values (based on the Shannon index of entropy) are plotted against taxon richness (as simple diversity). LycB90 sample numbers are shown next to the data points.

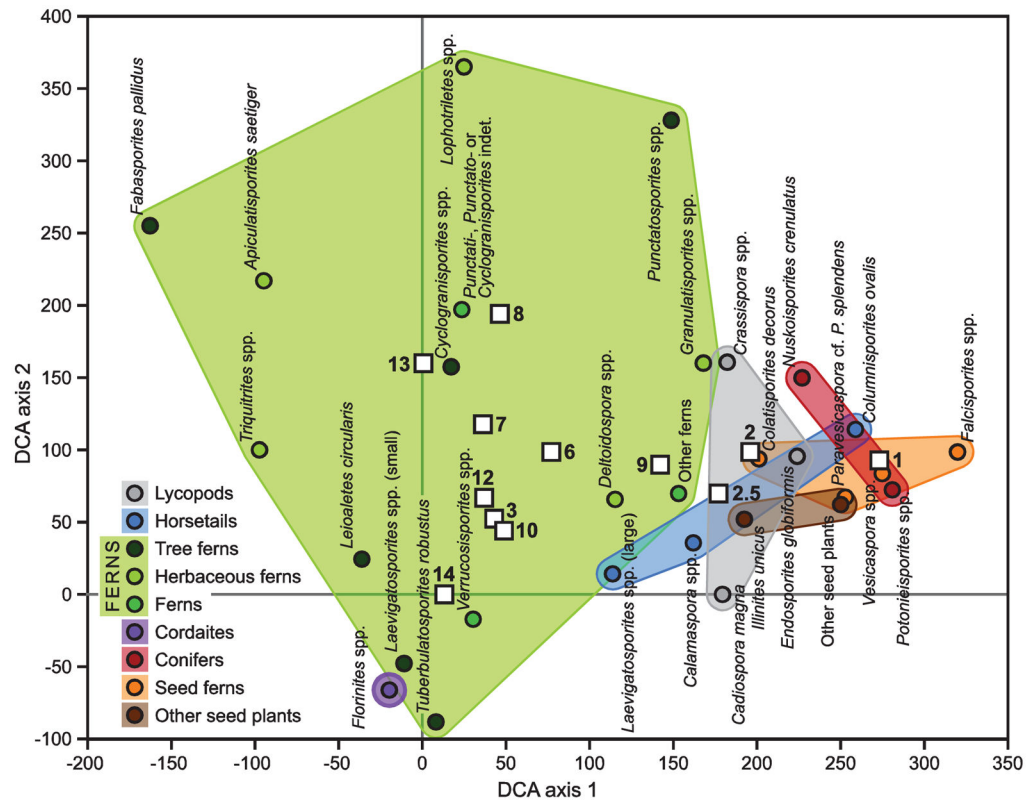


Fig. 5. Ordination of palynomorphs from the Lycopod B sequence, based on a Detrended Correspondence Analysis (DCA) of the data. Selected palynomorph taxa (or groups of taxa) are plotted as colored dots on the first two DCA axes, which respectively account for 26.4 and 10.5% of the variance in the species data. The palynomorphs are grouped in colored convex envelopes, based on their botanical affinity. In this biplot, samples are shown as white squares; their numbers refer to the ‘LycB90’ sample numbers.

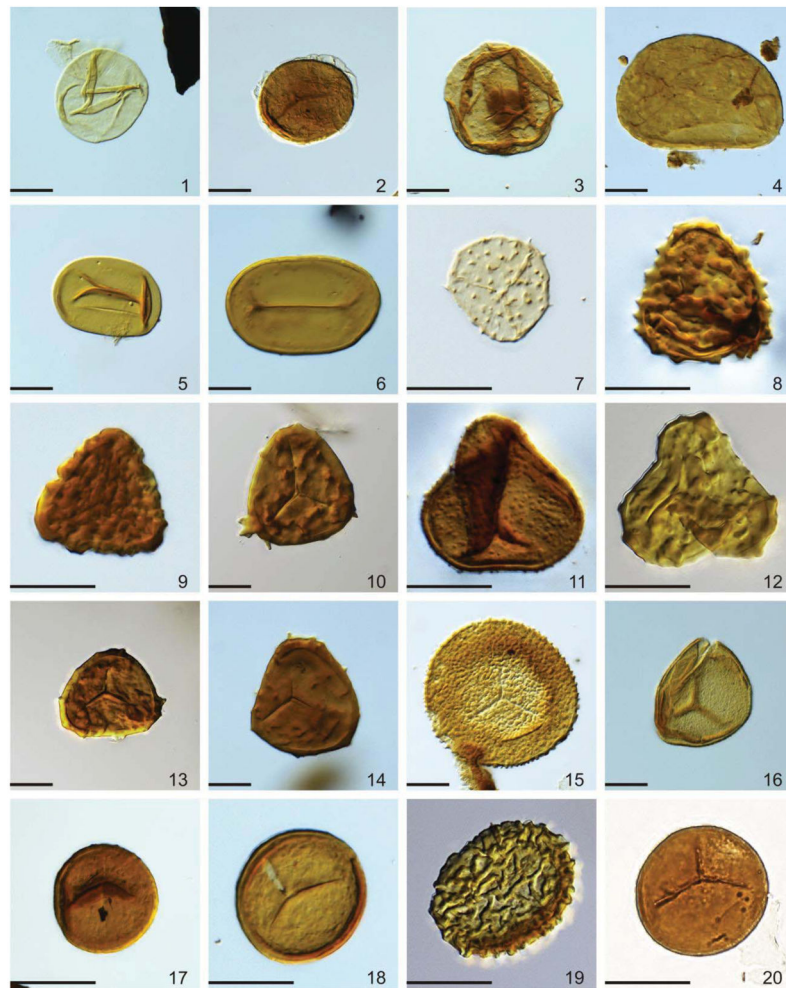


Plate 1

Plate I.

Selected simple spores from the Lycopod B East locality, Markley Formation, north-central Texas. Specimen names are followed by USNM numbers, slide code and England Finder graticule coordinates. Scale bar is 20 μ m.

1. *Leioaletes circularis* (USNM 546150, LycB90-12-1, B38-3)
2. *Diaphonosporites parvigracilis* (USNM 546151, LycB90-10-1, H45-4)
3. *Calamospora breviradiata* (USNM 546152, 40081-1, G44)
4. *Columinisporites ovalis* (USNM 546153, LycB90-2-6, L38-2)
5. *Laevigatosporites medius* (USNM 546154, LycB90-7-1, D62-4)
6. *Tuberculatosporites robustus* (USNM 546155, LycB90-10-3, T41-2)
7. *Anapiculatisporites vegrandis* (USNM 546156, TX2007-5-2, Q48-2)
8. *Converrucosporites* sp. (USNM 546157, LycB90-6 GG2, E18-2)
9. *Convolutispora* sp. (USNM 546158, LycB90-9-2, C43-2)
10. *Gillespiesporites venusta* (USNM 546159, LycB90-10-1, O51-4)
11. *Granulatisporites* sp. (USNM 546160, LycB90-6 GG2, P18-2)
12. *Gillespiesporites venustus* (USNM 546161, LycB90-10-1, W63-3)

13. *Triquitrites sculptilis* (USNM 546162, LycB90-7-1, Y62-1)
14. *Triquitrites spinosus* (USNM 546163, LycB90-10-3, O53)
15. *Verrucosiporites donarii* (USNM 546164, LycB90-14-1, S47)
16. *Cyclogranisporites aureus* (USNM 546165, LycB90-10-3, V37-4)
17. *Cyclogranisporites flavus* (USNM 546166, LycB90-8-2, D43)
18. *Cyclogranisporites minutus* (USNM 546167, LycB90-9-2, K55)
19. *Dictyomonolites swadei* (USNM 546168, LycB90-1-1, N41-1)
20. *Punctatisporites minutus* (USNM 546169, LycB90-10-1, V37-2)

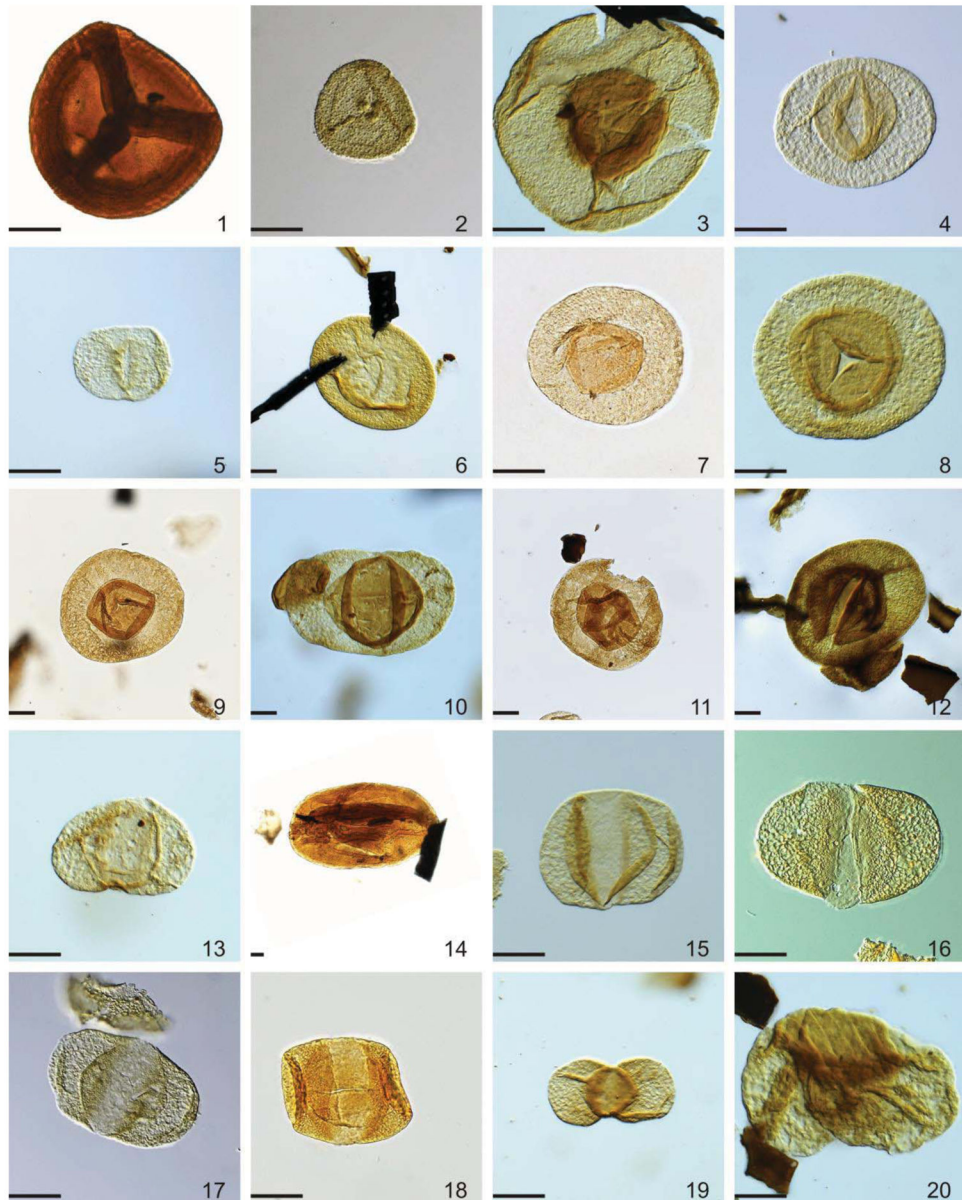


Plate 2

Plate II.

Selected camerate spores and pollen from the Lycopod B East locality, Markley Formation, north-central Texas. Specimen names are followed by USNM numbers, slide code and England Finder graticule coordinates. Scale bar is 20 μm .

1. *Cadiospora magna* (USNM 546170, LycB90-10-1, M35-2)
2. *Crassispora kosankei* (USNM 546171, LycB90-7-1, M56-4)
3. *Endosporites globiformis* (USNM 546172, LycB90-10-3, H47)
4. *Florinites mediapudens* (USNM 546173, LycB90-10-1, U37-2)
5. *Florinites millottii* (USNM 546174, LycB90-7-1, P60-2)
6. *Florinites pumicosus* (USNM 546175, LycB90-10-1, X43-1)

7. *Florinites volans* (USNM 546176, LycB90-101, D36-3)
8. *Nuskoisporites* sp. (USNM 546177, LycB90-10-3, S37-1)
9. *Nuskoisporites* sp. (USNM 546178, LycB90-7-1, X62-2)
10. *Potonieisporites elegans* (USNM 546179, LycB90-2.5, U46-1)
11. *Potonieisporites simplex* (USNM 546180, LycB90-1-1, U46-3)
12. *Potonieisporites* sp. (USNM 546181, LycB90-6-GG2, P17-1)
13. *Vesicaspora wilsonii* (USNM 546182, TX2007-5-2, Q54-1)
14. *Schopfipollenites ellipsoides* (USNM 546183, LycB90-7-1, X63)
15. *Alisporites* sp. (USNM 546184, LycB90-10-3, L34-2)
16. *Alisporites* cf. *plicatus* (USNM 546185, LycB90-1-1, K44-1)
17. *Falcisporites zapfei sensu* Jizba (USNM 546186, LycB90-1-1, S43-1)
18. *Illinites* cf. *unicus* (USNM 546187, LycB90-10-1, K58-3)
19. *Platysaccus* sp. (USNM 546188, TX2007-5-2, T39)
20. *Protohaploxypinus* sp. (USNM 546189, 2007-5-2, H45-1)

Table 1

Lycopod B identified pollen and spores and botanical affinity. First column: Taxonomic resolution: ● = known from a single order or family; ◎ = known from a single class, but in multiple or unknown orders; ○ = known from a single division, but in multiple or unknown classes; × = known from multiple divisions or division unknown; Second column: Taxa; Third column: (1) Literature references to in situ records and previous authors who have assigned particular spore/pollen taxa to macrofloral elements; (2) information where these micro-macro correlations were established (locality, area and age); (3) and comments on the reliability of correlations, indicating how trustworthy specific assignments to taxa are.

	Spore or (pre)pollen category	Botanical affinity
×	<i>Alisporites</i> cf. <i>plicatus</i> Jizba 1962	Peltaspermales (seed ferns) and Voltziales (conifers) <i>Alisporites</i> s.l. has been described <i>in situ</i> from the peltamales pollen organ <i>Pterispermotrobus</i> (Permian, Germany; Balme, 1995), pollen organ <i>Lelestrobus</i> (? Peltaspermales, Permian/Triassic, India; Srivastava, 1984), and Triassic <i>Corystospermales</i> (Osborn and Taylor, 1993). It has also been isolated from conifer cones, including <i>Ullmannia</i> (Voltziales, Permian, Germany; Florin, 1944; Potonié, 1962) and <i>Willsiostrobus</i> (Triassic, France; Grauvogel-Stamm, 1978).
×	<i>Anapiculatisporites vegrandis</i> (Upshaw et Creath) Ravn 1986	Botryopteridaceae (herbaceous ferns) and unknown Lycopsidea (lycopods) SEM studies have shown that spores found in <i>Botryopteris</i> sp. (Carboniferous, USA) belong to <i>Anapiculatisporites</i> (Balme, 1995), but it has also been also described from a lycopsid of unknown affinity (<i>Carinostrobus</i> , Carboniferous, USA; Baxter, 1971).
●	<i>Apiculatisporites aculeatus</i> (Ibrahim) Ravn 1986 <i>A. latigranifer</i> (Loose) Ravn 1986 <i>A. spinulistratus</i> (Loose) Ibrahim 1933 <i>A. variocorneus</i> (Sullivan) Ravn 1986 <i>A. variusetosus</i> (Peppers) Ravn 1986	Zygopteridales (herbaceous ferns) <i>Apiculatisporites</i> spores (including <i>A. spinulistratus</i>) were found <i>in situ</i> in <i>Corynepteris</i> (Carboniferous, USA, England, Germany and France; Brousmiche, 1983; Balme, 1995).
●	<i>Apiculatisporites saetiger</i> (Peppers) Ravn 1986	Zygopteridales (herbaceous ferns) <i>Apiculatisporites saetiger</i> spores have been found <i>in situ</i> in <i>Corynepteris</i> (Carboniferous, Scotland, Hemsley et al., 1994).
●	<i>Cadiospora magna</i> Kosanke 1950	Lepidodendrales: Sigillariaceae; Sigillaria (lycopods) <i>Cadiospora</i> is known from the heterosporous strobilus <i>Thomasostrobus</i> , which resembles those of <i>Sigillaria brardii</i> (Pennsylvanian; Czech Republic; Opluštil et al., 2009).
○	<i>Calamospora breviradiata</i> Kosanke 1950 <i>C. flexilis</i> Kosanke 1950 <i>C. parva</i> Guennel 1958 <i>C. pedata</i> Kosanke 1950 <i>C. straminea</i> Wilson et Kosanke 1944	Equisetales, Sphenophyllales (horsetails), and Noeggerthiales (progymnosperms) Carboniferous <i>Calamospora</i> is known <i>in situ</i> from strobili of Equisetales (e.g., <i>Calamostachys</i> , <i>Palaeastachya</i>) and Sphenophyllales (<i>Bowmanites</i>), and cones belonging to Noeggerthiales, of unknown affinity (e.g., USA, Germany, France, Czech Republic, China; for an overview see Balme, 1995; Taylor et al., 2009). <i>Calamospora</i> in Lycopod B probably do not represent Noeggerthiales; megafossils attributable to that group are rare or absent in the Texas flora.
×	<i>Colatisporites decorus</i> (Bharadwaj and Venkatachala) Williams, in Neves et al. 1973	? Lyginopteridales (seed ferns) The prepollen <i>Colatisporites</i> has been found in ovules of <i>Lyrasperma scotica</i> , but the pollen organs are unknown (Retallack and Dilcher 1988).
●	<i>Columinisporites ovalis</i> Peppers 1964	Sphenophyllales (horsetails) <i>Columinisporites</i> is known <i>in situ</i> from Euramerican Carboniferous sphenopsid cone taxa <i>Bowmanites</i> (England, Potonié, 1962), <i>Peltastrobus</i> (USA, Taylor, 1986), and <i>Sentisporites</i> (USA; Riggs and Rothwell, 1985).
×	<i>Convolutispora florida</i> Hoffmeister et al. 1955 <i>C. tessellata</i> Hoffmeister et al. 1955	Polypodiidae, Marattiales (both ferns) and Lyginopteridales (seed ferns) <i>Convolutispora</i> spores have been described <i>in situ</i> from Carboniferous Euramerican Zygopteridaceae, Botryopteridaceae, and Marattiales, and Lyginopteridales (Balme, 1995). In Lycopod B <i>Convolutispora</i> likely represents ferns.
●	<i>Crassispora kosankei</i> (Potonié et Kremp) Bhardwaj 1957 <i>C. annulata</i> Ravn 1979	Lepidodendrales: Sigillariaceae; Sigillaria (lycopods) Spores attributable to <i>Crassispora</i> (including <i>C. kosankei</i>) have been found <i>in situ</i> in Carboniferous <i>Sigillaria</i> strobili (<i>Mazocarpon</i> , <i>Sigillariostrobus</i> , <i>Megalocarpon</i> ; USA, England, Germany; for an overview see Opluštil and Bek (2009)).
×	<i>Cyclogranisporites aureus</i> (Loose) Potonie et Kremp 1955 <i>C. flavus</i> (Kosanke) Potonie et Kremp 1955	Marattiales (tree ferns) and ? Medullosales (seed ferns) Many species of <i>Cyclogranisporites</i> spores (including cf. <i>C. aureus</i> , <i>minutus</i> and <i>orbicularis</i>) have been found <i>in situ</i> in <i>Asterotheca</i> , <i>Scolecopteris</i> and other fertile fronds of Marattiales (USA, France, Germany; Pfefferkorn et al., 1971; Zdrov et al., 2006) and

	Spore or (pre)pollen category	Botanical affinity
	<i>C. microgranus</i> Bhardwaj 1957 <i>C. minutus</i> Bhardwaj 1957 <i>C. lasius</i> (Waltz) Playford 1962 (syn: <i>C. multigranus</i> Smith et Butterworth 1967) <i>C. obliquus</i> (Kosanke) Upshaw et Hedlund 1967 (syn: <i>Punctatisporites obliquus</i> Kosanke 1950) <i>C. orbicularis</i> (Kosanke) Potonié et Kremp 1955	tentative Medullosan pollen organ <i>Potoniaea</i> (Carboniferous, England; for an overview see Balme, 1995). In Lycopod B <i>Cyclogranisporites</i> likely represents ferns.
●	<i>Deltoidospora gracilis</i> (Imgrund) Ravn 1986 <i>D. sphaerotriangularis</i> (Loose) Ravn 1986	Polypodiidae (ferns) <i>Deltoidospora</i> is found a wide range of Mesozoic ferns, but has not been described from Paleozoic representatives. However, <i>Leiotriletes</i> , a junior synonym of <i>Deltoidospora</i> (Balme, 1995) has been reported in Zygopteridales (including spores similar to <i>L. sphaerotriangularis</i> , Carboniferous, England; Chaphekar and Alvin, 1972), and numerous Carboniferous Euramerican Botryopteraceae (including spores comparable to <i>L. sphaerotriangularis</i> , Carboniferous, USA; Eggert and Delevoryas, 1967). Several of these spores are likely immature; for an overview see Balme (1995).
×	<i>Diaphanospora parvigracila</i> (Peppers) Ravn 1979	Parent plants unknown These trilete spores have not been found <i>in situ</i> . They could represent one of a number of ferns or seeds ferns.
×	<i>Dictyomonolites swadei</i> Ravn 1986	Parent plants unknown These spores have not been found <i>in situ</i> . They could represent one of a number of ferns or seeds ferns, but their morphology (small, irregular amb, ornamented, monolete) suggests an association with Marattiales.
●	<i>Endosporites globiformis</i> (Ibrahim) Schopf et al. 1944	Isoetales; Chaloneria/Polysporia (lycopods) Known <i>in situ</i> from Late Pennsylvanian strobili of <i>Polysporia</i> (USA, United Kingdom, Czech Republic; Chaloner 1958b; Bek et al., 2008).
●	<i>Fabasporites pallidus</i> Clendening 1979	Marattiales (tree ferns) Spores assignable to <i>Fabasporites</i> have been found <i>in situ</i> in fertile <i>Acaulanium</i> fronds (Carboniferous, USA, Millay, 1977).
●	<i>Falcisporites zapfei</i> (Leschik) Klaus 1963	Peltaspermales and Corystospermales (seed ferns) <i>Falcisporites</i> has been found in a large number of Peltaspermales and some Corystospermales, albeit mainly from the Permian and younger. Permian taxa, including <i>Nidistrobis</i> and <i>Pteruchus</i> (both Permo-Triassic, India; see Balme (1995) and references therein). It is also known from the pollen organ <i>Permotheca</i> (Permian, Russia; Meyen, 1984; Naugolnykh, 2013).
●	<i>Florinites florinii</i> Imgrund 1960 <i>F. junior</i> Potonié et Kremp 1956 <i>F. mediapudens</i> (Loose) Potonié et Kremp 1956 <i>F. millottii</i> Butterworth et Williams 1954 <i>F. occultus</i> Habib 1966 <i>F. pumicosus</i> (Ibrahim) Schopf et al. 1944 <i>F. similis</i> Kosanke 1950 <i>F. visendus</i> (Ibrahim) Schopf et al. 1944 <i>F. volans</i> (Loose) Potonié et Kremp 1956	Cordaitales: Cordaites <i>Florinites</i> -type pollen has been described from several <i>Cordaitanthus</i> cones (Carboniferous; USA, France; for an overview see Balme, 1995).
●	<i>Gillespieisporites venustus</i> Clendening 1969 (?= <i>Triquitrites</i> spp., esp. <i>T. sculptilis</i>)	Gleicheniaceae (herbaceous ferns) These trilete acavate spores have not been found <i>in situ</i> . However, they closely resemble <i>Triquitrites</i> spores, which have been found <i>in situ</i> in the fern <i>Szea sinensis</i> (Gleicheniales, Permian, South China; Yao and Taylor, 1988).
×	<i>Granulatisporites adnatus</i> Kosanke 1950 (syn: <i>G. adnatooides</i> (Potonié et Kremp 1955) <i>G. parvus</i> Kosanke 1950	Lycopsidea, Filicopsida, Equisetopsida, Lyginopteridales <i>Granulatisporites</i> is an undiagnostic morphotaxon, known from very different plant groups (see Balme, 1995). However, the taxa found in Lycopod B likely represent herbaceous ferns. <i>G. adnatus</i> is found in <i>Botryopteris</i> (England; Holden, 1962) and spores similar to <i>G. parvus</i> in <i>Oligocarpia</i> (Sermayaceae, France; Grauvogel-Stamm and Doubringer, 1975; Brousmiche, 1983, Pšeni ka et al., 2005).
●	<i>Guthoerlisporites</i> sp.	? Peltaspermales (seed ferns) According to Balme (1995), some of the spores found <i>in situ</i> in <i>Schuetzia</i> are assignable to <i>Guthoerlisporites</i> (see information under <i>Wilsonites</i>).
×	<i>Hymenospora</i> sp. cf. <i>H. caperata</i> Felix et Burbridge 1967	Parent plants unknown These trilete cavate spores have not been found <i>in situ</i> . Their parent plant is unknown.
●	<i>Horriditriletes</i> sp.	Polypodiidae: Osmundales and unknown ferns

	Spore or (pre)pollen category	Botanical affinity
		Spores similar to <i>Horriditriteles</i> have been found <i>in situ</i> in <i>Skaaripteris</i> (Osmundales, Permian, Antarctica; Galtier and Taylor, 1994), and in ferns of unknown affinities (Permian, India, and Australia; Balme, 1995).
×	<i>Illinites unicus</i> Kosanke 1950	Voltziales (conifers) <i>Illinites</i> pollen has been described from the conifer pollen cone <i>Willisiostrubus</i> (Voltziales, Triassic, France; Grauvogel-Stamm and Grauvogel, 1973; Grauvogel-Stamm, 1978). They have not been found in Carboniferous or Permian pollen organs.
●	<i>Laevigatosporites globosus</i> Schemel 1951 (intergrades w/ <i>C. obliquus</i>) <i>L. minimus</i> (Wilson et Coe) Schopf et al. 1944 <i>L. minor</i> Loose 1934	Marattiales (tree ferns) Both <i>L. globosus</i> and <i>minimus</i> have been isolated from <i>Scolecopteris</i> fronds (Marattiales, Carboniferous; USA, Canada; Pfefferkorn et al., 1971; Millay and Taylor 1984; Pšenicka et al., 2003). Small <i>Laevigatosporites</i> (30–35µm) are generally assigned to Marattiales and larger ones to Sphenophyllales (Ravn, 1986; Libertín et al., 2014).
●	<i>Laevigatosporites desmoinesensis</i> (Wilson et Coe) Schopf et al. 1944 <i>L. maximus</i> Loose 1934 em. Potonié et Kremp 1956 <i>L. medius</i> Kosanke 1950 <i>L. vulgaris</i> (Ibrahim) Ibrahim 1933	Sphenophyllales (horsetails) Several Sphenophyllales produce large monoete spores (35µm) with ridged perispores (<i>Columinisporites</i>). When the perispore is not preserved the spores are morphologically compatible with the dispersed spore genus <i>Laevigatosporites</i> (e.g., Playford and Dino, 2000; Balme, 1995; Libertín et al., 2014).
×	<i>Leioaletes circularis</i> Ravn et Fitzgerald 1982	? Marattiales (tree ferns) Ravn (1986) compares <i>L. circularis</i> to spores described <i>in situ</i> from <i>Radstockia</i> (Carboniferous, USA; Taylor, 1967). However, Libertin et al. (2014) consider <i>Leioaletes</i> to represent immature spores of <i>Laevigatosporites</i> or <i>Latisporites</i> .
●	<i>Lophotriteles granoornatus</i> Artüz 1957 <i>L. varispinosus</i> Peppers 1970	Botryopteridaceae (herbaceous ferns) <i>Lophotriteles</i> spores have been described from several Carboniferous taxa, e.g. <i>Botryopteris</i> , <i>Psalioclaena</i> , <i>Sphyropteris</i> , and <i>Renaultia</i> (USA, England, Germany, France; Remy and Remy, 1957; Good, 1981; Millay and Taylor, 1982; Potonié, 1962; Brousmiche, 1986; Balme, 1995).
●	<i>Microreticulatisporites nobilis</i> (Wicher) Knox 1955	Botryopteridaceae and Gleicheniaceae (herbaceous ferns) <i>Microreticulatisporites</i> spores have been found in <i>Botryopteris</i> (Botryopteridaceae, Carboniferous, USA and France; for an overview see Balme, 1995) and <i>Radiitheca</i> (Gleicheniaceae, Carboniferous, France and Czech Republic; Brousmiche et al., 1997).
●	<i>Nuskosporites crenulatus</i> Wilson 1962	Voltziales (conifers) The prepollen produced by members of the Late Permian conifer genus <i>Ortiseia</i> fall within the dispersed pollen genus <i>Nuskosporites</i> (Clement-Westerhof, 1984; Poort et al., 1997). <i>N. crenulatus</i> was likely also produced by a conifer.
×	<i>Paravesicaspora</i> cf. <i>P. splendens</i> (Leschik) Klaus 1963	Parent plants unknown (but seed plant based on morphology) This pollen type has not been found <i>in situ</i> , but the morphology closely resembles that of <i>Vesicaspora</i> and may represent Callistophytaceae or Peltaspermales, which have similar, alveolate bisaccate or pseudobisaccate, sulcoid pollen. In any case, it almost certainly represents a seed fern.
×	<i>Pityosporites</i> sp. cf. <i>P. westphalensis</i> Williams 1955	Parent plants unknown (but seed plant based on morphology) <i>Pityosporites</i> pollen has been found <i>in situ</i> in the gymnosperm microsporophyll <i>Pramelreuthia</i> (Triassic, USA; Ash and Litwin, 1996). The alveolar bisaccate morphology indicates that this form is produced by a seed plant, most likely a seed fern.
×	<i>Platysaccus saarensis</i> (Bharadwaj) Jizba 1962	Parent plants unknown (but seed plant based on morphology) <i>Platysaccus</i> has been found in cones associated with the Triassic seed fern <i>Dicroidium</i> (Corystospermaceae) (South Africa, Anderson and Anderson, 1983). The parent plants of the Carboniferous forms are unknown, but the alveolar bisaccate morphology indicates that it represents a seed plant, most likely a seed fern.
●	<i>Potonieisporites novicus</i> Bharadwaj 1954 <i>P. bharadwaji</i> Remy et Remy 1961 <i>P. elegans</i> (Wilson and Kosanke) Wilson et Venkatachala 1964 <i>P. simplex</i> Wilson 1962	Voltziales (conifers) The prepollen <i>Potonieisporites</i> was produced by members of several Pennsylvanian and Early Permian walchian conifer families, including Emporiaceae, Bartheliaceae, Thucydiaceae, Utrechtiaceae (e.g., Hernandez-Castillo et al. 2001; Rothwell et al., 2005).
○	<i>Protohaploxypinus</i> sp.	Glossopteridales and Peltaspermales (seed ferns) <i>Protohaploxypinus</i> pollen has been found in Permian pollen organs associated with Gondwanan Glossopteridales (e.g., Gould and Delevoryas, 1977; Zavada, 1991; Lindström et al., 1997). <i>Protohaploxypinus</i> was found <i>in situ</i> in pollen organ <i>Permotheca</i> , and in association with Peltaspermalean cuticles in a coprolite (Russia, Gomankov and Meyen, 1986; Meyen, 1997). Their parent plants in the Euramerican realm are, however, unknown.
×	<i>Punctatisporites edgarensis</i> Peppers 1970	Filicopsida, Equisetopsida, Cycadopsida, Noeggerathians, and Calamopityales

	Spore or (pre)pollen category	Botanical affinity
	<i>P. flavus</i> (Kosanke) Potonié et Kremp 1955 <i>P. glaber</i> (Naumova) Playford 1962 [syn: <i>P. curviradiatus</i> Staplin 1960] <i>P. obesus</i> (Loose) Potonié et Kremp 1955 <i>Punctatisporites minutus</i> (Kosanke) Peppers 1964 <i>Punctatisporites aerarius</i> Butterworth et Williams 1958 <i>Punctatisporites nitidus</i> Hoffmeister et al. 1955	Mature Carboniferous forms resembling <i>Punctatisporites</i> have been described from many plant groups (for an overview see Balme, 1995). <i>Punctatisporites aerarius</i> has been reported from <i>Scolecopteris majopsis</i> (Lesnikowska, 1989; see also Eble et al., 2003). <i>P. obesus</i> is known <i>in situ</i> from <i>Bowmanites</i> (sphenophylls, Czech Republic; Libertín et al. 2008). However, most of the species of <i>Punctatisporites</i> in the Lycopod B flora likely represent Marattiales or herbaceous ferns (Ravn, 1986).
●	<i>Punctatisporites punctatus</i> Ibrahim 1933 <i>P. rotundus</i> Bhardwaj 1957 em. Alpern et Doubinger 1973	Marattiales (tree ferns) <i>Punctatisporites</i> has been reported <i>in situ</i> from several Marattialean <i>sporangia</i> (USA, Pfefferkorn et al., 1971; France, Germany, Spain; for an overview see Balme, 1995).
×	<i>Pustulatisporites</i> sp. cf. <i>P. papillosus</i> (Knox) Potonié et Kremp	Parent plants unknown These spores have not been found <i>in situ</i> . They could represent one of a variety of ferns or seeds ferns.
×	<i>Reinschospora speciosa</i> (Loose) Schopf et al. 1944	Parent plants unknown These trilete spores have not been found <i>in situ</i> . However, most likely they represent some kind of fern or lycophyte.
×	<i>Reticulatisporites reticulatus</i> (Ibrahim) Ibrahim 1933	Sphenophyllales (horsetails) and unknown ferns <i>Reticulatisporites reticulatus</i> is known from <i>Bowmanites</i> cones (Sphenophyllales, Carboniferous, Czech Republic, Bek and Libertín, 2010), and in sporangial aggregates of unknown filicoid affinity (<i>Eopteridangium</i> , Carboniferous, USA; Andrews and Agashe, 1962; Potonié, 1967).
×	<i>Rugospora gracilirugosa</i> Ravn 1986 <i>R. radiata</i> Ravn et Fitzgerald 1982	Parent plants unknown These acavate trilete spores have not been found <i>in situ</i> . They could represent one of a variety of ferns or seeds ferns.
○	<i>Sahnispores</i> sp. cf. <i>S. saarensis</i> Bharadwaj 1954	Voltziales (conifers) These monoete bisaccate pollen have not been found <i>in situ</i> . However, they bear a close resemblance to <i>Potonieisporites</i> (Walchian Voltziales).
●	<i>Schopfipollenites ellipsoides</i> (Ibrahim) Potonié et Kremp 1954	Medullosales (seed ferns) <i>Schopfipollenites</i> (<i>Monoletes</i>) type pollen has been found <i>in situ</i> in <i>Aulacotheca</i> , <i>Bernalthia</i> , <i>Dolerotheca</i> (Carboniferous; USA, United Kingdom, France; e.g., Millay and Taylor, 1979; Taylor and Rothwell, 1982; Balme, 1995).
●	<i>Spinospores exiguus</i> Upshaw and Hedlund 1967	Marattiales (tree ferns) Spores resembling <i>Spinospores exiguus</i> have been described from <i>Scolecopteris monothrix</i> (Millay, 1979, Millay and Taylor, 1984).
×	<i>Tantillus triquetrus</i> Felix et Burbridge 1967	Parent plants unknown These acavate trilete spores have not been found <i>in situ</i> . They could represent one of a variety of ferns or seeds ferns, but in the Lycopod B flora most likely represent an herbaceous fern.
●	<i>Thymospora obscura</i> (Kosanke) Wilson et Venkatachala 1963 <i>T. thiesseii</i> (Kosanke) Wilson et Venkatachala 1963	Marattiales (tree ferns) <i>Thymospora</i> (including <i>T. obscura</i> and <i>thiesseii</i>) are known from synangia of fertile marattialean fronds (USA, France, Germany; Doubinger and Grauvogel-Stamm, 1971; Millay 1979; Lesnikowska and Willard, 1997).
●	<i>Triquitrites sculptilis</i> Balme 1952 em. Smith et Butterworth 1967 <i>T. spinosus</i> Kosanke 1943	Gleicheniaceae (herbaceous ferns) <i>Triquitrites</i> spores have been found <i>in situ</i> in <i>Szea sinensis</i> (Gleicheniaceae, Permian, South China; Yao and Taylor, 1988).
●	<i>Tuberculatosporites robustus</i> (Kosanke) Peppers 1970	Marattiales (tree ferns) <i>Tuberculatosporites</i> spores are known <i>in situ</i> from the following Marattiales: <i>Pecopteris</i> (Carboniferous, France), <i>Qasimia</i> (Permian, Saudi Arabia), and <i>Scolecopteris</i> (Carboniferous USA). For an overview see Balme (1995).
×	<i>Verrucosisporites donarii</i> Potonié et Kremp 1955 <i>V.</i> sp. cf. <i>V. morulatus</i> (Knox) Potonié et Kremp 1955 em. Smith et Butterworth 1967 <i>Verrucosisporites verrucosus</i> (Ibrahim) Ibrahim 1933 <i>V. microtuberosus</i> (Ibrahim) Smith et Butterworth 1967	Zygotpteridales, Marattiales, Lyginopteridales, Medullosales, Isoetales The genus <i>Verrucosisporites</i> is an undiagnostic morphotaxon that has been attributed to, Marattiales, Lyginopteridales, Medullosales and even Isoetales (for overview see Balme, 1995). Most or all of the <i>Verrucosisporites</i> spores in Lycopod B likely represent Zygotpteridales and Marattiales. <i>V. verrucosus</i> has been reported <i>in situ</i> from <i>Corynepteris</i> (Zygotpteridales, Carboniferous, U.S.A, Pfefferkorn et al., 1971). Spores resembling <i>V. microtuberosus</i> were produced by <i>Acitheca</i> (Marattiales, Carboniferous, Canada, Czech Republic; Zodrow et al., 2006).

	Spore or (pre)pollen category	Botanical affinity
○	<i>Vesicaspora wilsonii</i> Schemel 1951 em. Wilson et Venkatachala 1963 <i>V. ovata</i> (Balme and Hennelly) Hart 1960	Callistophytales and Peltaspermales (seed ferns) <i>Vesicaspora</i> has been found <i>in situ</i> in pollen organs (<i>Idanothekion</i>) borne on <i>Callistophyton</i> pinnules (Carboniferous, USA, Millay and Taylor, 1979; Rothwell 1981), and in the pollen organs <i>Pterispermotrobus</i> (Peltaspermales, Permian, Germany, Kerp, 1988) and <i>Permotheca</i> (Permian, Russia; Krassilov et al., 1999; Zavalova and Van Konijnenburg-van Cittert, 2011).
×	<i>Waltzispora sagittata</i> Playford 1962 <i>Waltzispora prisca</i> (Kosanke) Sullivan 1964	Parent plants unknown These trilete spores have not been found <i>in situ</i> . They could represent one of a variety of ferns or seeds ferns.
●	<i>Wilsonites circularis</i> (Guennel) Peppers et Ravn, in Ravn 1979	? Peltaspermales (seed ferns) <i>Wilsonites</i> is known from pollen organs (<i>Schuetzia</i>) associated with <i>Sphenopteris germanica</i> ; a potential peltasperm (Permian; Germany; Remy and Rettschlag, 1954; Balme, 1995).
×	<i>Zosterosporites triangularis</i> Kosanke 1973	Parent plants unknown These trilete spores have not been found <i>in situ</i> . They could represent one of a variety of ferns or seeds ferns.