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Research paper

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

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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 megaflora 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. Megafloral 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 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 megafloral 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.

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 walchian 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 and Darrah, 1989; DiMichele et al., 2010; Falcon-Lang and Pendleton, 2011; Falcon-Lang et al., 2011; Bashforth et al., 2014). Based on ecomorphological characters, especially of conifers (Kerp, 1996, 2000) and their sedimentological context (Rueger, 1996; Falcon-Lang and Pendleton, 2011), these gymnosperm-dominated

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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; Montañez et al., 2007; Fielding et al., 2008; 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 pCO_2 (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 10^6 and 10^5 years (Heckel, 2008; Tabor and Poulsen, 2008; Eros et al., 2012; Pointon 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 pCO_2, 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 (Falcon-Lang, 2004; Feldman et al., 2005). 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 (Peyser 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 (Falcon-Lang and Pendleton, 2011; Gastaldo and Demko, 2011). 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; Tabor et al., 2013; Dimichele, 2014). 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; Tabor et al., 2008; Looy, 2013; Looy and Duijnstee, 2013; Tabor et al., 2013; Looy and Stevenson, 2014), 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 (Gzehlian-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 rccords 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 Pangaean 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