C. R. Geoscience 346 (2014) 159–168

Contents lists available at ScienceDirect

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External Geophysics, Climate

# Middle and Late Pennsylvanian cyclothems, American Midcontinent: Ice-age environmental changes and terrestrial biotic dynamics

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ARTICLE INFO

*Article history:*
Received 13 January 2014
Accepted after revision 13 March 2014
Available online 10 August 2014

*Keywords:*
Climate
Coal
Cyclothem
Paleoecology
Pennsylvanian

ABSTRACT

The Pennsylvanian portion of the Late Paleozoic Ice Age was characterized by stratigraphic repetition of chemical and siliciclastic rocks in the equatorial regions of the Pangean interior. Known as "cyclothems", these stratigraphic successions are a $10^5$ yr-record of glacial waxing and waning, superimposed on longer term, $10^6$ yr intervals of global warming and cooling and a still longer term trend of increasing equatorial aridity. During periods of maximum ice–minimum sea level, the interior craton was widely exposed. Epicontinental landscapes were initially subjected to dry subhumid climate when first exposed, as sea level fell, but transitioned to humid climates and widespread wetlands during maximum lowstands. During interglacials (ice-minima) seasonally dry vegetation predominated. The wetland and seasonally dry biomes were compositionally distinct and had different ecological and evolutionary dynamics.

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## 1. Introduction

The Pennsylvanian portion of the Late Paleozoic Ice Age (approx. 323–299 Ma) was characterized by regular waxing and waning of Southern Hemisphere continental glaciers (Fielding et al., 2008; Isbell et al., 2003a). In order to provide a precise definition of time scales for Earth's warming and cooling events, we use terminology as outlined in Cecil (2013). ***Glacial stage*** (shortest scale of a single glacial–interglacial cycle, $10^5$ yr) pacing may have been on the rhythm of Milankovich-band orbital frequencies (Heckel, 2008). These individual glacial–interglacial cycles were superimposed on ***glacial epoch*** scale (longer-term, $10^6$ yr) intervals of global warming and cooling (Birgenheier et al., 2009, Joeckel, 1999), further superimposed on a ***period-scale*** trend of long-term equatorial drying and warming ($10^7$ yr) (Tabor and Poulsen, 2008). Regularity of climate and sea-level changes at the glacial-stage scale has permitted correlation across North America (Cecil et al., 2003a) and even across the Euramerican portions of Pangea in deposits of paralic (marine influenced) basins from the American Midcontinent to the Donets Basin (Eros et al., 2012; Heckel et al., 2007). Patterns of equatorial sea-level change strongly correlate with inferred polar ice volume on both stage and epoch temporal scales (Rygel et al., 2008).

Equatorial climate changed in concert with ice volume and sea level, most notably the patterns, durations and amounts of equatorial rainfall (Fig. 1B). These changes occurred on all time scales from glacial–interglacial stages (Cecil et al., 2003a; Horton et al., 2012), to epoch-scale intervals of global warming and cooling (e.g., Cecil, 1990; Rygel et al., 2008), to a period-scale, long-term trend of warming and drying (Cecil, 1990; Montañez and Poulsen, 2013, Tabor and Poulsen, 2008). Climate change has been

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http://dx.doi.org/10.1016/j.crte.2014.03.008
1631-0713/Published by Elsevier Masson SAS on behalf of Académie des sciences.

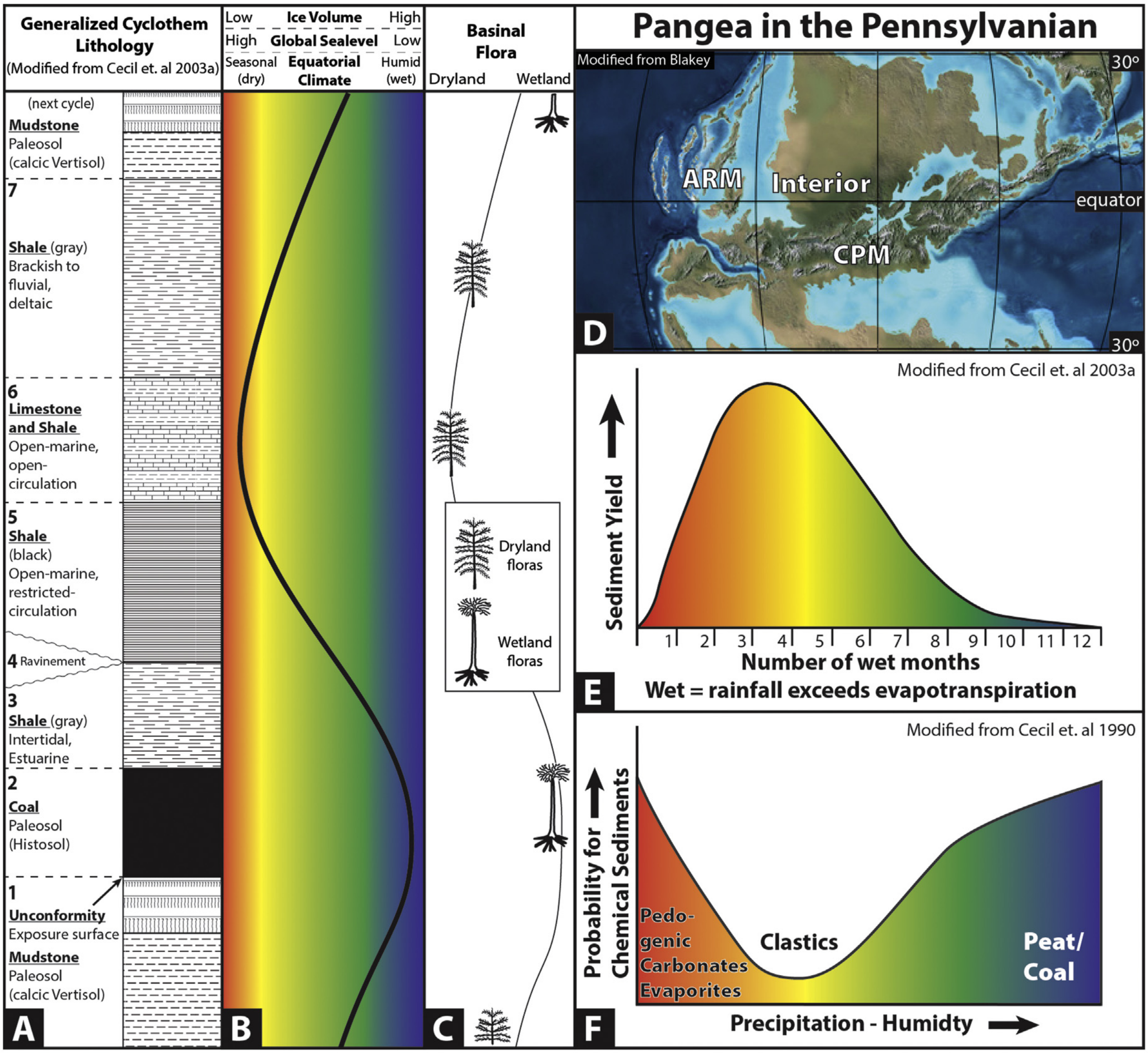


**Fig. 1.** (Color online.) Interior Pangean cyclothem. A. Stratigraphic architecture of a complete glacial–interglacial, stage-scale cycle. 1-paleosol; 2-coal; 3-esturaine gray-shale wedge; 4-ravinement surface; 5-marine black shale; 6-marine limestone; 7-deltaic and nearshore siliciclastics. B. Patterns of change in ice volume, sea level, equatorial climate. C. Equatorial floristic changes, tracking climate change. D. Pennsylvanian Pangea. E. Climate-Siliciclastic sediment yield relationship. F. Climate-Sediment type relationship.

integrated into the broader understanding of sedimentary and biological dynamics of the Late Paleozoic Ice Age (LPIA). Climate has a strong, direct effect on lithofacies patterns in both limnic (non-marine) and paralic basins. Lithologies such as coal (formerly peat–a Histosol) and mineral paleosols directly record climatic conditions. There are strong climatic effects on siliciclastic sediment availability and transport (Cecil et al., 2003b) (Fig. 1E), the extent to which environments of deposition are mixed and oxygenated, and the chemical conditions. Where siliciclastic input is absent or minimal, and where necessary chemical and physical conditions are met, climate becomes an important control on carbonate formation (Fig. 1F) (Cecil and Dulong, 2003; Cecil et al., 2003b).

Pangean plants and animals also strongly reflected and tracked environments (Fig. 1C), at all spatio-temporal scales (DiMichele et al., 2009, 2010; Falcon-Lang and DiMichele, 2010; Opluštil et al., 2013). Thus, many paleontological patterns, including evolutionary dynamics, are direct reflections of regional climatic patterns, controlled by global-scale factors. Here we review the lithological signature and biological effects of LPIA glacial–interglacial cyclicity on landscapes of the vast, flat, central-western portions of the Pangean supercontinent, between the Central Pangean Mountains and Ancestral Rockies (Fig. 1D). These patterns are expressed primarily during the late Middle and Late Pennsylvanian in the Western Interior (Midcontinent) and Eastern Interior (Illinois) basins, USA, more so than in the Appalachian basin. It is there that the "cyclothem" concept developed (see Cecil et al., 2003a; Heckel, 1990; Langenheim and Nelson, 1992; Weller, 1931). This region is well suited for revealing ice-age climate and sea level dynamics in equatorial latitudes: Paralic character and low elevations permitted far reaching sea-level fluctuations. Great distance from mountain ranges in the eastern and western interior areas greatly reduced habitat variation and effects of uplands on climate and biological patterns. Great flatness of the cratonic surface created widespread environmental spatio-temporal uniformity.

## 2. Record and dynamic drivers of glacial–interglacial cycles

### 2.1. The Cyclothem

Glacial–interglacial cyclicity has a distinctive, if geographically and environmentally variable, lithological signature. Such successions can be entirely marine (e.g., Elrick and Scott, 2010), entirely terrestrial (e.g., Eble et al., 2006), or mixed (e.g., Heckel, 2008), and subject to local tectonic, and climatic overprints. We focus on mixed terrestrial-marine cyclothems, as found in cratonic settings, particularly of the Eastern Interior basin USA, located between the more marine influenced Western Interior and more terrestrial Appalachian basins. Over time, the high relief, eroded surface of the Mid-Carboniferous unconformity (Bristol and Howard, 1974) was in-filled across the American Midcontinent. This lowered the relief of the cratonic platform over which glacial–interglacial cycles were expressed (e.g. McKee and Crosby, 1975; Watney et al., 1989), resulting in alternation of marine and terrestrial environments in the Western and Eastern Interior regions of Pangea during each glacial–interglacial cycle (Archer et al., 1994a); here marine rocks generally dominate total stratigraphic thickness of a cycle (Fig. 1A).

Terrestrial facies include mineral paleosols (Fig. 1A-1), developed on previously deposited sediments, often succeeded by Histosols (peat, now coal) (Fig. 1A-2). Siliciclastic deposits with fluvial channel-form geometries may occur at the same stratigraphic level as the mineral paleosol, interpreted as drainages on the terrestrial landscape contemporaneous with the paleosol surface (Davies and Gibling, 2013). Plant fossils indicative of seasonally dry conditions may occur in these fluvial deposits, but usually are rare (Feldman et al., 2005). During peat development, some channels continued to be active, likely as blackwater rivers, transitioning to mud-filled estuaries during transgression (Archer et al., 2014). Estuarine tidal deposits, referred to as Gray Siltstone Wedges (GSW) (Archer and Kvale, 1993), may be present locally between the coal bed and overlying marine strata (Fig. 1A-3). GSWs are laterally continuous with deposits that backfill the courses of the former drainages through the peat swamp (Elrick and Nelson, 2010). Local gradational contacts between the coal bed and the base of the GSW are common and often include upright, fossil trees, and rich accumulations of plant compression fossils representative of wetland environments (Archer et al., 1994b).

The base of the marine portion of a cyclothem is marked by a transgressive erosional surface (a ravinement) above the coal bed and GSW (Liu and Gastaldo, 1992). This surface may be overlain by a relatively thin "transgressive" marine limestone (Heckel, 2008), which is more common in Western Interior cycles than in the Eastern Interior or Appalachians. Variably developed, the transgressive limestone is often absent or represented only by shell hash. Where limestone is absent, the ravinement surface may be marked by local accumulations of phosphatic nodules or pyrite-permineralized plant remains. A marine, black, generally fissile shale typically lies in sharp, erosional contact with the underlying strata, immediately above the ravinement surface (Fig. 1A-4) and may be extremely widespread (e.g., Cecil et al., 2003a; James and Baker, 1972). In the Western and Eastern Interior basins, black shale is overlain by open-marine limestone in conformable contact (Fig. 1A-5). The black shale and overlying limestone are generally the most widespread marine beds.

In many successions, coarsening upward, gray-shale overlies the open-marine limestone, (Fig. 1A-6). These deposits are likely of fluvial-deltaic origin. It is on this heterogeneous surface, following exposure during sea level regression and early lowstand, that the terrestrial part of the next cycle, the paleosol, is developed.

#### 2.1.1. The flat craton and water depth

During the late Middle and Late Pennsylvanian, the Pangean interior was a low relief surface with a gradient possibly $< 1$ m/km, with a few areas, e.g. the Ozark Dome in Missouri, of tectonically created higher relief (McKee and Crosby, 1975). As a consequence of flat topography, small sea-level changes likely had large effects on coverage of the craton by marine waters. Low gradient and lack of significant topography would have allowed unimpeded airflow patterns over large areas. From a biological viewpoint, this regionally flat terrain suggests limited elevational effects on regional climate. Spatial disruption of lowstand ecosystems would have been widespread and extensive in response to drowning during times of rising sea level. Furthermore, due to covariation of climate and sea level with ice volume, ecosystems on the craton were affected by climate changes at the same time they were forced to move physical location by associated sea-level change.

#### 2.1.2. Terrestrial facies I: Paleosols

Recent studies of coal underclays (e.g., Cecil et al., 2003a; Driese and Ober, 2005; Rosenau et al., 2013) indicate complex polygenetic histories, starting as mineral paleosols and transitioning to peat formation. In soil moisture terms (Cecil, 2013, p. 23; Soil Survey Staff, 1998), as related to rainfall, these soils were first well drained, with Ustic soil moisture (seasonal dryness), induced by seasonal rainfall under subhumid climate. Increasing rainfall under moist subhumid to humid climate produced Udic soil moisture (evenly distributed annual rainfall equal to evapotranspiration). Finally, Aquic soil moisture (saturated) developed, rainfall exceeding evapotranspiration for most of the year (humid to perhumid climate). Paleosols also reflect the period-scale drying trend. Through Early and early Middle Pennsylvanian, most paleosols indicate initially Udic soil conditions, becoming Aquic as rainfall increased and seasonality decreased during the glacial phase of a cycle (Driese and Ober, 2005). In late Middle and Late Pennsylvanian, however, paleosols with vertic features and calcium carbonate concentrations indicate initially Ustic soil moisture regimes (wet during the growing season but dry most of the year); these paleosols formed under seasonal, dry sub-humid to semi-arid climatic regimes. Carbonate concentrations reflect periods during which evapotranspiration strongly exceeded moisture throughput, resulting in pedogenic carbonate mineral deposition in the soil (Driese et al., 2005). In all of these polygenetic paleosols, later stages of development record translocation of clays, various minerals and iron downward through the soil, overprinting earlier soil profiles. This indicates increase in moisture throughput, reduction in seasonality and gradual but persistent increase in the consecutive number of months where rainfall exceeded evapotranspiration. Translocation of iron, in particular, known as gleying, indicates the existence of acidic (facilitating conversion of insoluble ferric to soluble ferrous iron), well drained (facilitating translocation of soluble iron) conditions. The acidity most likely results from organic matter buildup (a response to rainfall-induced increase in vegetative cover) in the soil O horizon, accompanied by formation of weak organic acids. As precipitation increased to humid or perhumid conditions, mineral substrates became permanently water logged, and clastic swamps, organic mucks, and shallow lakes developed on the mineral paleosol surface. In such wetland deposits characteristic plant fossils may be present. The deposits sometimes grade without break into coal beds, indicating a conversion of clastic swamps to peat swamps. Most often, however, the contact between the top of the paleosol and the bottom of the coal bed is relatively sharp. Variation in the paleosol-coal bed contact captures the meter-to-decimeter scale, topographic irregularity of the mineral-paleosol, pre-peat swamp landscape and indicates a rapid shift from mineral soil formation to widespread development of organic Histosols and peat formation (Fig. 1A-1).

Penecontemporaneous paleochannels, including extensive floodplains, are associated with the mineral paleosol interval. Rarely mapped in detail, a few examples (Allen et al., 2011; Bragonier et al., 2007; Feldman et al., 1995; Potter, 1963) indicate that floodplains were dynamic and that principle rivers sometimes deeply incised the craton.

### 2.1.3. *Terrestrial facies II: Coal*

Despite much study of coal, both as a rock and a former peat deposit, many misconceptions and misunderstandings remain. We address some of those here (Fig. 1A-2).

We differentiate peat from organic muck, and confine our discussion to those peats that could give rise to commercial grade coal beds. This means low mineral content of the original peat ($< 20\%$), leading to low ash content ($< 40\%$) of the resulting coal. Organic-rich deposits with mineral matter $> 20\%$ likely yielded black shales or organic-rich gray shales.

As a former peat deposit, coal beds are likely to have had highly complex histories of formation, including periods of drowning and decay, removal of peat by fires, and intervals of rapid organic accumulation (DiMichele and Phillips, 1994). In cases of repeated disruption of peat formation, multi-benched coals resulted. Cecil et al. (1985) summarized conditions of peat formation. For peat to form in warm equatorial regions precipitation must exceed evapotranspiration during most of the year or the water table will fall and organic destruction by fires and organism-mediated decay will occur. Equatorial rainfall must exceed evapotranspiration for $>$ 10 months (humid to perhumid climates) for rates of organic accumulation to exceed destruction (Fig. 1F). Peat may form any place and any time these conditions are met, regardless of sea level, elevation, or some degree of topographic irregularity, including areas of free drainage, as evidenced by modern peat formation on windward slopes of the British Isles. Even under high, aseasonal rainfall, thickness and degree of decay of peat bodies will vary according to the local physical and chemical conditions (including no peat formation). Much evidence suggests that any given Pennsylvanian coal bed is time equivalent or nearly so throughout its extent: the peat formed as a blanket deposit over an entire landscape. Indications of this include such features as coal beds that extend across entire basins, regional-scale volcanic ash partings in a number of coal beds (Greb et al., 1999; Lyons et al., 1992; Opluštil et al., 2007; Wang et al., 2012), or widespread mineral partings that separate petrographically and palynologically distinctive coal benches (Eble et al., 2006; Greb et al., 2003). As a consequence, initiation and maintenance of peat-forming conditions call for a mechanism that can systematically raise water tables over a vast area of the craton effectively simultaneously. The most likely mechanism is humid to perhumid climate (see Cecil, 2003, p. 16), amplified by the exceedingly low relief and consequent poor drainage. Rivers draining Pennsylvanian peat swamps during the wettest phases of glacial–interglacial cycles appear to have carried low sediment loads and, at times, to have been "black water", carrying most of their load as dissolved solids (Nelson et al., 2008). Such patterns reflect large reductions in sediment mobility caused by dense lowland vegetation cover. In the Pangean interior, this was combined with great distances to upland-region sediment sources. A modern parallel is the extremely low sediment load in Indonesian rivers under humid to perhumid climates, including those draining peat swamps (Cecil et al., 2003b). There, even in areas of steep elevational gradients, vegetation cover induced by high rainfall strongly limits erosion and sediment runoff into streams due to dense penetration and binding of the soil by plant roots (Cecil et al., 2003b).

### 2.1.4. *Transitional terrestrial-to-marine facies*

The most poorly studied lithofacies of a cyclothem is the Gray Siltstone Wedge (Fig. 1A-3). These deposits, of limited areal extent, back fill and occur lateral to peat-contemporaneous rivers that were converted to estuaries during sea-level transgression. Sediment comprising the GSWs may have been generated, at least in part, by tidal erosion during initial flooding of the craton. During these early phases of sea-level rise and onset of cratonic flooding, climate began a shift to increasingly seasonal, subhumid (Cecil et al., 2003a; Horton et al., 2012). Such climate change across the equatorial region reduced vegetation density on the landscape, permitting significant increases in the sediment load of stream drainages (Cecil and Dulong, 2003). In combination with rising sea level, sediment was pushed inward at drowning river mouths, causing rapid aggradation, and the development of large mudflats flanking estuaries (Archer, 2004). Peat swamps were converted to short-lived clastic swamps. Evidence points to very high rates of sediment accumulation (Archer and Kvale, 1993; Archer et al., 2014), which account for the burial of upright trees and the abundant preservation of plant remains (e.g., DiMichele et al., 2009; King et al., 2011). Recent studies suggest that GSW deposits formed in a series of episodic meltwater pulses (Archer et al., 2014), during which sediment accumulation rates in and lateral to estuaries were rapid and high (Archer and Greb, 2012). Fossil evidence of in situ preserved plants indicates that the GSW was initially fresh-water. Salinities became brackish as sediment accumulated, indicated by invertebrates such as linguloids, myelinid pelecypods, and eurypterids. There is no evidence of normal marine salinities during GSW deposition.

### 2.1.5. Marine facies

Onset of marine conditions in a cyclothem is often marked by a widespread erosional or "ravinement" surface that scours the top of the coal bed and the GSW (Liu and Gastaldo, 1992). This can be deduced from the truncation of coal laminae and by erosional remnants of GSW sediments in areas more distal from channels (DeMaris et al., 1983). The ravinement surface is caused by tidal energy during the widespread flooding of epicontinental basins. Although a thin transgressive limestone, often a shell-hash lag, may be present immediately above the ravinement surface, more typically this surface is overlain directly by a fissile, marine black shale. Black shales had complex depositional and geochemical histories (Algeo et al., 2004; Schultz and Coveney, 1992) and anoxic to dysoxyic conditions are indicated by high organic content and limited bioturbation. The physical conditions necessary to generate low oxygen bottom waters have been debated. Prevailing models estimate 70–100 m water depths (e.g., Heckel, 1977) and place these shales near marine high-stand (e.g. Algeo et al., 2004). Other studies (e.g., Cecil et al., 2003a; Coveney et al., 1991; Zangerl and Richardson, 1963), including those of Gondwanan ice volumes (Isbell et al., 2003b), suggest much shallower water. Low oxygen, shallow-depth bottom waters have been ascribed to limited mixing (Cecil et al., 2003a), reflecting low surface wind velocities and limited mixing during early transgression, when strong polar high-pressure fronts continued to restrict cross-equatorial migration of the Intertropical Convergence Zone (ITCZ), creating equatorial doldrums. Holterhoff and Cassady (2012) also ascribe black-shale deposition to climatic conditions, arguing that under wet, weakly seasonal climates, sea-bottom anoxia is created by a hyposaline cap from terrestrial runoff that causes nutrient loading of surface waters and high productivity. In all these models, despite slow, limited siliciclastic input, there is no carbonate production. Again, climate-driven scenarios offer solutions that water depth does not; the initiation of carbonate formation begins with the onset of drier climatic conditions, and greater mixing of the water column caused by break down of the doldrums and increased surface winds (Cecil et al., 2003a) (Fig. 1A-4, 5, 6).

Equatorial climates became most strongly seasonal (dry sub-humid to semi-arid) during late transgression and into highstand. Modeling studies (Horton et al., 2012) indicate the highest absolute levels of annual rainfall during late transgression to early highstand phases of the cycle, but with strong seasonality. During this time period and as noted above, marine limestones became widespread across the craton. Subsequent aridity during late highstand and during regression reflects the largest seasonal excursions of the ITCZ during a glacial–interglacial cycle, a response to retreat of polar ice masses and associated Arctic high-pressure (Cecil et al., 2003a). This also can be visualized as a weakening of equatorial Hadley cell circulation (Peyser and Poulsen, 2008), resulting in increased seasonality and reduction of equatorial precipitation. Also, during interglacials more extensive seasonal migrations of the ITCZ create more intense equatorial winds, resulting in greater mixing and water column oxygenation, a suggested explanation for the shift from black-shale deposition to limestone formation (Cecil et al., 2003a).

Deltaic deposits of regional extent, emplaced during late highstand and early regression, often succeed open marine strata. With initiation of ice buildup, equatorial climates began to see increased precipitation, though of a seasonal nature, due to reductions in the amplitude of ITCZ annual migrations and general Hadley cell strengthening (Horton et al., 2012). The result was significant increases in siliciclastic sediment transport. The biota of these deposits varies widely from marine to brackish fauna; the plant component is largely wetland, reflecting the high water tables of the delta top, but rarely may reveal species typical of seasonally dry climates, reflecting the general background conditions (Pšenička et al., 2011).

It is partially upon these deltaic deposits that the terrestrial phase of the next glacial cycle began. As sea level receded (regression due to ice buildup), a terrestrial surface emerged across the basinal lowlands of the craton. Paleosols indicate that this initially occurred under a seasonally dry climate (Driese and Ober, 2005; Feldman et al., 2005. Joeckel, 1989; Rosenau et al., 2013), becoming more humid as ice volume increased and sea level fell.

## 2.2. A note on accommodation space and inter-basin correlations

There was great variation in the rates and amounts of accommodation created within different Pennsylvanian lowland basins. For example, the Lower and lower Middle Pennsylvanian of the Appalachian basin is nearly 1200 m thick, whereas it is only 200 m thick in the Illinois basin. Foreland basin subsidence may have been the dominant Appalachian basin tectonic control on accommodation space whereas sediment loading and other unknown tectonic forces controlled Eastern and Western Interior basin subsidence (McKee and Crosby, 1975). In contrast, in the Central Pangean Mountain regions of Central Europe, there were highly variable rates of sediment accumulation, some basins being entirely intra-montane and potentially high altitude (Opluštil, 2005). Nonetheless, the effects of tectonics are sufficiently time averaged in large, paralic, equatorial basins to permit marine-organism-based correlations across wide areas for many time intervals of the Pennsylvanian; individual cycles and stacks of cycles have been correlated from the American Western Interior to as far east as the Donets basin of the Ukraine (Eros et al., 2012; Heckel et al., 2007; Rosscoe and Barrick, 2013), particularly in the late Middle and Late Pennsylvanian. Correlations among American basins based on marine organisms and coal palynology (Cecil et al., 2003a; Peppers, 1996) have made linkages between most of the major and many of the minor cycles.

## 3. Glacial–interglacial cyclicity and the equatorial terrestrial biota

Pennsylvanian glacial–interglacial cycles had major effects on both terrestrial and marine biotic dynamics in equatorial latitudes. Although we focus here on the terrestrial, there are parallels in the marine realm. Most importantly, there were environments that oscillated greatly in areal extent, particularly terrestrial peat swamps and marine black-mud ocean bottoms. For most of the time represented by a cyclothem, these occasionally widespread environmental-types either did not exist or were confined to small areas. At other times, and for relatively shorter periods, they were present over huge areas.

Is the Pleistocene to Recent ice age an analogue for the Pennsylvanian, and vice versa? Certainly, there are strong parallels in the fundamental allocyclicity of the system on large spatio-temporal scales. However, there are major differences in continental configuration, size and location of interior continental flatlands and positions of mountain ranges, which create distinct patterns of ocean and atmospheric circulation. In other words, glacial–interglacial cycling played out in different regions at these different times. Furthermore, and perhaps of even greater importance–flowering plants have dominated tropical ecosystems since the Late Cretaceous. Recent studies of Boyce and colleagues (Boyce et al., 2010) indicate angiosperms can pump water from the soil to the atmosphere via evapotranspiration at rates far exceeding any other plant group (though see Wilson et al., 2008, on medullosan water relations). Consequently, modern-type rainforests, where over 70% of rainfall is "recycled" via high altitude cooling and condensation of evapotranspirative moisture, may not have existed before the evolution of angiosperms. The implication is that the rainfall fueling Pennsylvanian peat swamps may have been generated largely by atmospheric convective precipitation, the plants contributing little to the creation of moisture clouds to support rainforest architectures. Thus, without flowering plants, interglacials of our modern terrestrial equatorial regions would be significantly more seasonally dry than at present.

One final caveat is needed when comparing and contrasting the Late Paleozoic and modern worlds–biodiversity. Late Paleozoic terrestrial ecosystems had many fewer species than those younger than Early Cretaceous (e.g., Wing and DiMichele, 1995). In contrast, the number of dominant major phylogenetic groups (traditional Linnean classes) in the landscape was much greater than today (DiMichele and Phillips, 1996). The consequences of this are several and, as yet, only peripherally explored by paleobotanists as follows:

- strong niche conservatism. Resource partitioning appears to track phylogenetic relatedness–specific evolutionary lineages had distinct ecologies within terrestrial landscapes. This phenomenon has been labeled "phylogenetic niche partitioning" (e.g., Webb et al., 2002) and is present as far back into the land plant record as anyone has looked for it (Hotton et al., 2001);
- niche breadth of late Paleozoic species may have been greater than that found in most modern species, on average. There were fewer players in the game, but that game–resource competition and niche partitioning–was played by the same rules as today. At present, this is virtually unexplored;
- most kinds of plants relied on wind for some phase of their life cycle: pollination, seed dispersal or spore dispersal. A few relied on water for dispersal. Reliance on wind, or on water at certain life-cycle phases, created the potential for extensive gene flow. High gene flow can be expected to reduce rates of speciation and, thereby, rates of radical morphological or physiological innovation. As far as we know, only one study has addressed this (Raymond and Costanza, 2007), by examining rates of species turnover in pteridosperms (non-wind dispersed large seeds and pollen) vs. other Pennsylvanian seed-plant groups (wind dispersed);
- plant-animal interactions were much more limited in scope than in post-Paleozoic systems (Labandeira and Sepkoski, 1993). In the Paleozoic there were less herbivory and fewer kinds of herbivory, limiting the transfer of plant primary productivity to consumer portions of food webs. In addition, there is no definitive evidence for pollination of plants by animal vectors;
- Pennsylvanian equatorial terrestrial ecosystems were broadly of two types: those composed of wetland plants and those composed of plants adapted to seasonal drought (there probably were several kinds of these depending on the degree of moisture stress) (DiMichele et al., 2008). These can be considered unique biomes. There is little evidence to suggest large populations of species adapted to seasonal drought within areas of widespread wetlands; such occurrences as are known appear to represent allochthonous elements introduced by long-distance transport. In contrast, wetland elements are a nearly ubiquitous autochthonous to parautochthous background in seasonally dry landscapes (e.g., Bashforth et al., 2014). This asymmetry is expected. Widespread wetlands call for great areal coverage of the continental interior by humid to perhumid climates. Under such conditions, drainage effects caused by local topographic irregularity are greatly suppressed, leaving few places where plants requiring seasonal drought might flourish. In contrast, seasonally dry landscapes, particularly those of sub-humid climates, are sprinkled with local areas of high water table, such as stream

margins, intra-channel bars, lakesides, and coastal lagoons, providing patches and corridors of wetlands for obligately wetland species.

There are two major issues to examine in the terrestrial equatorial regions when considering the biological consequences of the strongly linked oscillations in climate and sea level that accompanied glacial–interglacial cycles:

- what happened to the wetland species, and the ecosystems in which they thrived, during periods of widespread seasonal aridity in the equatorial regions?
- Conversely, where were seasonally dry taxa during periods of widespread wetland development? Empirical data suggest that these two kinds of ecosystem did not simply oscillate back and forth in space through time as climate changed. Rather, the two vegetation types and their component species pools had different dynamics between intervals of abundance in the lowlands (DiMichele et al., 2010).

### 3.1. Wetland Fate

Empirical evidence (e.g., Bashforth et al., 2014; Dolby et al., 2011) and climate models (Horton et al., 2012; Poulsen et al., 2007) suggest absence during interglacial periods of equatorial areas sufficiently wet to support large tracts of wetland-specialist vegetation. Consequently, it is most likely that populations of wetland plants broke up and survived in refugial areas: stream- and lake-sides, in braidplains, along coastlines (Falcon-Lang and DiMichele, 2010). Localized occurrences of wetland species within dryland assemblages, and occurrence of wetland palynomorphs within strata deposited during interglacial intervals (Falcon-Lang et al., 2009; Hawkins et al., 2013; Stephenson et al., 2008), indicate the presence of wetland-plant populations in seasonally dry landscapes. However, the likelihood of organic-matter preservation is greatly reduced in seasonally dry settings (Gastaldo and Demko, 2011) by:

- low probability of short-term burial below mean low water table accompanied by high rates of degradation;
- low likelihood of subsequent intermediate term burial by marine water (if such landscapes occur between highstand and early lowstand, during regression).

Based on these boundary conditions, wetland vegetation would have reassembled from refugia during each recurrence of widespread, equatorial humid climate. Despite these regular oscillations there is high compositional and dominance-diversity conservatism of wetland vegetation (e.g., DiMichele et al., 2009). The cause of this conservatism may be the dominance of wetland disassembly-reassembly cycles by lottery dynamics:

- during contraction into refugia, the dominant species of the preceding widespread wet period were most likely to dominate in refugia;
- these most numerically abundant species then reasserted proportional dominance as populations expanded out of refugia during the next wet interval. The main limiting variable was dispersal capacity.

Because most wetland plants had wind-dispersed pollen or microspores (Phillips et al., 1985; Taylor and Millay, 1979), the possibility was high for maintaining genetic continuity among populations physically fragmented by widespread seasonal drought. The great exception to this generality is the medullosan pteridosperms, which had poorer pollen dispersal than other seed plants, due to the large size of the grains; consequently, they should have had more population isolation and higher rates of speciation (Raymond and Costanza, 2007). Nearly all the dominants have propagules that were either water (lycopsids–e.g., Phillips, 1979; pteridosperms–e.g., DiMichele et al., 2006) or wind (tree ferns–e.g., Willard et al., 2007; cordaitaleans–e.g., Souza and Iannuzzi, 2012) dispersed. Thus, no group in particular may have had a signal advantage during the onset of renewed wet climates, which would favor reassembly controlled largely by initial numbers. However, because of the periodic oscillations in population sizes, the entire system had a built-in hypersensitivity to extreme interglacial aridity, during which populations could be squeezed to extinction or regional extirpation. This apparently did cause occasional widespread ecosystem reorganization at environmental threshold points (DiMichele et al., 2010; Heckel, 1991; Phillips et al., 1974).

### 3.2. Seasonally dry vegetational dynamics

There appear to have been permanent, large populations of seasonally-dry-adapted plants in western equatorial Pangea and parts of the Central Pangean Mountains (e.g., Bashforth et al., 2014; Cridland and Morris, 1963; Falcon-Lang and Bashforth, 2005; Tidwell et al., 1992; Uhl et al., 2004). As a result, it would seem that these low diversity, nearly entirely wind pollinated and dispersed, largely seed-plant floras simply spread across the land surface in response to climate changes, following topographically constrained routes. They exhibit, as a consequence, long-term compositional homogeneity. And the change from cordaitalean to coniferalean dominated assemblages is long and drawn out over many millions of years, tracking a long-term trend in increasing equatorial aridity at all phases of glacial–interglacial cycles (e.g., Tabor and Poulsen, 2008).

As a consequence of these large standing populations, seasonally-dry-adapted vegetation appears to have experienced limited evolutionary innovation within any given species pool. Rather, innovations appear to have originated from the progressive colonization of environments with increasingly greater moisture and, possibly/probably, temperature extremes, and other environmental extremes, such as salinity (e.g., Poort and Kerp, 1990). This implies that survival of new body plans, physiologies, and reproductive strategies was most likely to occur where competition from large, standing populations of ancestral forms was lowest, at the ragged, gradational margins of environmental tolerance of the species (DiMichele and Aronson, 1992). It is in the deposits formed in these progressively more extreme environments that progressively more phylogenetically advanced elements of respective clades are found (e.g., conifers–Kerp, 1996; Looy, 2007; gigantopterids–DiMichele et al., 2011; peltasperms–Poort and Kerp, 1990; Naugolnykh and Kerp, 1996; cycadophytes–DiMichele et al., 2001; corystosperms–Kerp et al., 2006).

Because of the poor preservation of seasonally dry floras during Pennsylvanian, and even Permian time, it is challenging to assemble a coherent picture of their evolutionary history. However, by documenting their biogeographic occurrences and linking them to indicators of climate, it is possible to develop an idea of the environmental factors affecting their evolutionary dynamics. These appear to have been different from those affecting the plants of the wetland biome and reflect mainly dry-season length or confinement to special edaphic conditions.

## 4. Conclusions

The Pennsylvanian and Early Permian glacial world has many parallels to the Pleistocene, Holocene and Recent. Cyclic waxing and waning of glaciers, and periodic intervals of warming with near disappearance of polar ice, created a dynamic world–geologically and biologically. The equatorial regions of this time hosted the well-known peat (coal) swamps. They also, however, were home to vast tracts of plants adapted to seasonal drought. Understanding the relationships of these distinct biomes relies upon an understanding of the climatic dynamics associated with glacial–interglacial cycles.

The evidence presented herein suggests strong linkages between ice volume, sea level, climate and patterns of lithological variation in the sedimentary rock record. This system is represented in the interior of Pangea by the repetitious spatio-temporal stratigraphic packages of so-called "cyclothems". Models that link ice-volume, atmospheric circulation and sea-level change, placing maximum rainfall and maximum wetland development at lowstand, best explain the data. Minimum seasonality occurred during glacial maximum and at sea-level lowstand. During interglacials through early parts of succeeding glacial phases, seasonally dry climates prevailed and the exposed parts of basinal lowlands were colonized by seasonally dry vegetation. A full cycle may have represented about 100,000 years.

Vegetation and, most likely, associated terrestrial vertebrate and invertebrate faunas, closely followed the changes in climate state across the Pangean equatorial interior. These distinct biomes shared few taxa in common and had distinct ecological and evolutionary dynamics.

## Acknowledgements

We thank Sylvie Bourquin for the invitation to submit this paper. Research supported by U.S. Geological Survey, Smithsonian Institution, and State of Illinois. We thank many colleagues for sharing their ideas and expertise.

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