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DYNAMICS OF COAL-AGE TROPICAL VEGETATION

WETLAND-DRYLAND VEGETATIONAL DYNAMICS IN
THE PENNSYLVANIAN ICE AGE TROPICS

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Premise of research.   The Late Paleozoic Ice Age was the last extensive pre-Pleistocene ice age. It includes many climate changes of different intensities, permitting examination of many and varied biotic responses. The tropical Pennsylvanian Subperiod, usually visualized as one vast wetland coal forest, in fact also was dominated, periodically, by seasonally dry vegetation that, in turn, covered most of the central and western Pangean supercontinent. Equatorial wetland and dryland biomes oscillated during single glacial-interglacial cycles. This recognition changes understanding of the Coal Age tropics; examination of their spatiotemporal patterns indicates that these vegetation types responded differently to global environmental disturbances and long-term trends and points to potentially different underlying controls on evolutionary histories of their component lineages.

Methodology.   This study is based on the published literature and on examination of geological exposures and fossil floras, mainly from North America but also from other parts of the world.

Pivotal results.   Wetlands and seasonally dry habitats were equally part of the Coal Age Pangean tropics. They dominated these landscapes at different times, under different climatic regimes. Wetland vegetation was likely forced into refugia during seasonally dry (subhumid to semiarid) parts of glacial-interglacial cycles; it reemerged/reassembled during wet (humid to perhumid) periods. Seasonally dry vegetation resided permanently in areas of western and central Pangea and in microhabitats within the Central Pangean Mountains. Both floras had lower biodiversity than modern floras in similar habitats. The wetland flora species pool was more phylogenetically disparate than any modern vegetation. In contrast, seasonally dry floras were dominated by seed plants. These biomes responded differently to acute environmental changes and chronic long-term aridification.

Conclusions.   From ecological or evolutionary perspectives, the present-day world is but one possibility. Lower-diversity worlds such as the late Paleozoic, with a rich spectrum of environmental variations, offer insights into relationships between organisms and environments that expand understanding of these phenomena and enlarge our sense of what is possible or probable as we look to the future.

Keywords: Pennsylvanian, tropics, upland, Coal Age, paleoecology, climate, biodiversity.

Introduction

The Pennsylvanian Subperiod of the Carboniferous is, perhaps, best known colloquially as the Coal Age and envisioned as a time when the tropical land surface was covered in vast forested wetlands, many sitting on meters-deep peat deposits. Thanks to more than 250 yr of collecting in coal mines and from natural exposures, plant fossils from this time period populate the drawers of nearly every major museum in Europe and North America, many private collections, and displays in schools and private homes. No image of the deep past may be more iconic in the public mind than that of a dark, forbidding forest filled with strange plants, primitive amphibians, spiders

the size of dinner plates and dragonflies with meter-wide wingspans. So much has been collected and published about Coal Age plants and animals that one might reasonably conclude that specialists have reached a broad general understanding of the organisms and the ecology of the time, vividly portrayed in dioramas. However, this is not so.

Over the past 40 yr the foci of Pennsylvanian tropical paleobotany, while continuing with traditional systematic and evolutionary studies, have multiplied, expanding particularly into the geological sciences. Greater appreciation of the importance of the late Paleozoic as an ice age has spurred interest in climate as a dynamic variable; of changing atmospheric composition; and of the covariant changes in sea level, climate, and sedimentation patterns. Paleobotanists have brought to their work much greater appreciation of the effects of large-scale, long-term geological factors, such as mountain building and changes in continental positions through time. Further-

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more, biological understanding has come to include much more about physiology and development, changing and enlivening the ways in which we understand the plants themselves.

There is insufficient space in this review to go into depth in all these areas. Nonetheless, several basic patterns are emerging that illustrate our vastly changed appreciation of the dynamics of this time period as well as the basic ecology of different kinds of Pennsylvanian-age tropical vegetation.

1. The Pennsylvanian was a time of dozens of glacial advances and retreats, leading to tens of millions of years of climate and sea level oscillations. There is a hierarchy of such oscillations, beginning with 10^5-yr-duration glacial-interglacial cycles superimposed on more widely spaced 10^6-yr periodic intervals of intense global warming and nearly complete global deglaciation, with these then further superimposed on a long-term multimillion-year trend of tropical aridification.

2. Polar and high-elevation 10^5-yr cyclic changes in ice volume (glacial-interglacial cycles) were accompanied by changes in climate, sea level, and sedimentation that were strongly expressed in the tropics. In great contrast to what is understood, or at least broadly promulgated, about the tropics of our modern ice age, the wettest times in the Pennsylvanian tropics seem to have corresponded to glacial maxima and the driest times to interglacial periods.

3. The concept of an invariably ever-wet tropical realm is incorrect. Reflecting the strong climatic oscillations on glacial-interglacial timescales of 10^5 yr, vast areas of the Pennsylvanian tropics alternately harbored wetland and dryland floras. The preservational potential of these two kinds of vegetation was vastly different; strong selection against the preservation of dryland vegetation makes its sporadic occurrences appear anomalous. This apparent peculiarity of seasonally dry vegetation in coal-bearing strata is belied, however, by increasing appreciation of paleosols in and sequence stratigraphic architectures of these strata.

4. Vegetation characteristic of seasonally dry climates may have dominated the lowland tropics for as long as or longer than wetlands during any given 10^5-yr glacial-interglacial cycle. From a biogeographic viewpoint, resident populations of plants that preferred seasonal aridity appear to have lived permanently in the western and central regions of the Pangean tropics and possibly within microhabitats in parts of the Central Pangean Mountains. The evolutionary and ecological implications of these dynamics and the associated patterns are profound.

5. The densest of tropical vegetation, from the wettest time periods, may have been much more open than previously envisioned, produced much less moisture feedback to the atmosphere through evapotranspiration than modern tropical forests, and had patterns of tree growth and turnover unlike any we know today. In this sense, there may have been no true tropical "rain forests" during the Pennsylvanian, at least not as we understand them and their water cycle in the modern flowering-plant-dominated world.

6. The biodiversity of the Pennsylvanian, and the late Paleozoic in general, was much lower than that of today in all habitat types. It might be expected, therefore, that certain aspects of ecosystem structure and function were simpler than or different from today and that many species may have encompassed broader resource spectra than typical of most extant plants.

All told, this is a world about which a great deal is known, perhaps more than any other period in deep-time, terrestrial earth history. Though much remains to be learned, we do know that this time has many parallels with our modern world. The physical earth dynamics are quite similar to those of today. Vegetational responses to those environmental cycles provide us with insights into the behavior of biological systems under the kinds of background conditions and likely disruptive influences faced at the present time. Like few other times in the past, the Late Paleozoic Ice Age (LPIA) is a part of deep-time history to which we can turn if we want to calibrate, test, or more fully develop models of how the glacial-interglacial earth and its biota function.

Environmental Framework of the Pennsylvanian Glacial World

The Late Paleozoic Ice Age

During the late Paleozoic, the terrestrial surface of the Earth was largely aggregated into the megacontinent of Pangea (fig. 1). A string of eastern microcontinents and islands circumscribed an eastern ocean, Tethys, and surrounding Pangea was the vast stretch of the Panthalassic Ocean. The Pangean landmass is subdivided into four regions based on both latitude and paleogeography. The north and south temperate latitudes fall within Angara and Gondwana, respectively. The eastern tropical microcontinents comprise Cathaysia. The principal tropical continental landmass is Euramerica, encompassing essentially what today are the northernmost parts of South America and Africa, most of North America, and Europe. Due to the way in which the continents were sutured together, a significant mountain range, the Central Pangean Mountains, ran roughly NE-SW through the center of Euramerica. Though reconstructions show this mountain range as synchronously present throughout its length, it appears, rather, to have been uplifted and eroded earlier in its eastern regions than in the west (Krohe 1996; Hatcher 2002; Hnat et al. 2012). It is subdivided into several subregions; here only the Variscans and Appalachians are referred to.

The LPIA comprises the most significant set of boundary conditions for the physical and biotic dynamics and patterns of the Pennsylvanian and Early Permian (Fielding et al. 2008). The earliest development of major volumes of ice took place at the end of the Devonian and continued into the earliest Mississippian (Brezinski et al. 2008; Isaacson et al. 2008). This was followed by an interval of intense drying and warming at tropical and paratropical latitudes (Cecil 2004). Ice reappeared in the middle Mississippian and continued into the Middle Permian (Montañez et al. 2007; Fielding et al. 2008; Bishop et al. 2009; Isbell et al. 2012; Montañez and Poulsen 2013), a period of as much as 65 million years in duration, during which time moisture returned to the equatorial region. Figure 2 outlines the geological stratigraphic terms used in this article.

The LPIA is complex, which is no surprise, given its long history. Recent studies indicate that LPIA ice was not organized into a massive south-polar ice cap but consisted instead of numerous ice centers (Isbell et al. 2003a, 2003b; Fielding et
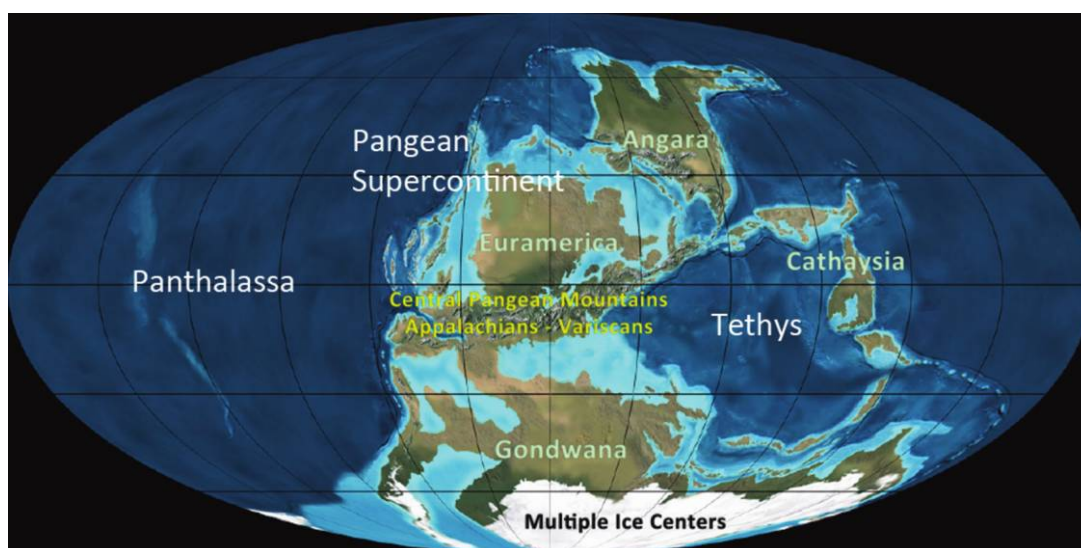
Fig. 1 Pennsylvanian world and major geographic features. Note that current research does not support the existence of a large Southern Hemisphere ice sheet but rather a number of smaller ice centers. Base map courtesy of Ron Blakey, Northern Arizona University.

al. 2008). The LPIA also was marked by considerable fluctuations in ice volume and the location and number of ice centers, which have been documented most extensively in the Southern Hemisphere (Montañez and Poulsen 2013 provide a summary and integration of current knowledge of the LPIA, including extensive literature citations). In the tropics, these ice volume changes are reflected in a hierarchy of global sea level fluctuations of different magnitudes, from glacial-interglacial cycles, on 10^5 timescales (Heckel 2008; Horton et al. 2012), to longer-term trends during which glacial and nonglacial phases alternated on timescales of 10^6 yr (Birgenheier et al. 2009), reflecting periods of more extensive global warming and cooling (Haq and Schutter 2008; Heckel 2008; Rygel et al. 2008). These patterns are further superimposed on a long-term trend of warming and aridification in the tropics (for summary see Tabor and Poulsen 2008). The more distant driver of these changes, on all scales, appears to have been atmospheric CO_2 concentration (Peyser and Poulsen 2008; Horton et al. 2012; Montañez and Poulsen 2013), which was, on average, at one of the lowest concentrations of the Phanerozoic (Berner and Kothavala 2001; Royer et al. 2007).

Tropical Cyclic Sedimentation: Background

The Pennsylvanian portion of the LPIA left a distinctive lithological signature on the continental shelves of tectonically active, equatorial depositional basins (figs. 3, 4). Described as cyclothems for the repeated cyclic pattern of different lithologies, representing different kinds of original depositional environments (for historical summaries see Langenheim and Nelson 1992; Archer 2009), these signature deposits were first recognized in the Illinois Basin (Udden 1912), described in detail by Wanless and Weller (1932) and attributed to polar glaciation by Wanless and Shepard (1936). A cyclothem is a record of covarying changes in sea level, climate, and sedimentation patterns (Cecil et al. 1985, 2003b; Tandon and Gib-

ling 1994; Heckel 1990, 2008; Cecil and Dulong 2003), representing cycles of approximately Milankovich durations of 100,000 and 400,000 yr (Heckel 1986; Pointon et al. 2012). Recent studies have demonstrated that specific cyclothems, representing individual glacial-interglacial cycles, can be correlated across much of the expanse of the Euramerican equatorial
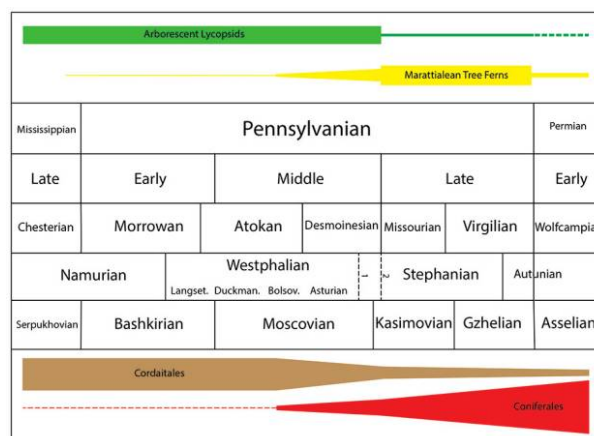

Fig. 2 Stratigraphic names used in the Pennsylvanian and temporally adjacent geological intervals. For details see Davydov et al. (2012). Relative abundance of arborescent lycopsids (green) and marattialean tree ferns (yellow) in wetlands and cordaitaleans (brown) and conifers (red) in seasonally dry environments. Chesterian-Virgilian = names used in North American stratigraphy. Namurian-Autunian = European names used for terrestrial strata. 1 = Westphalian-Stephanian as defined by some stratigraphers. 2 = Traditional Westphalian-Stephanian boundary as defined by the 1935 Herleen Congress (see Falcon-Lang et al. 2012). It is essential, when reading the literature, to understand which of these boundaries is being used. Serpukovhian-Asselian = international stratigraphic units.
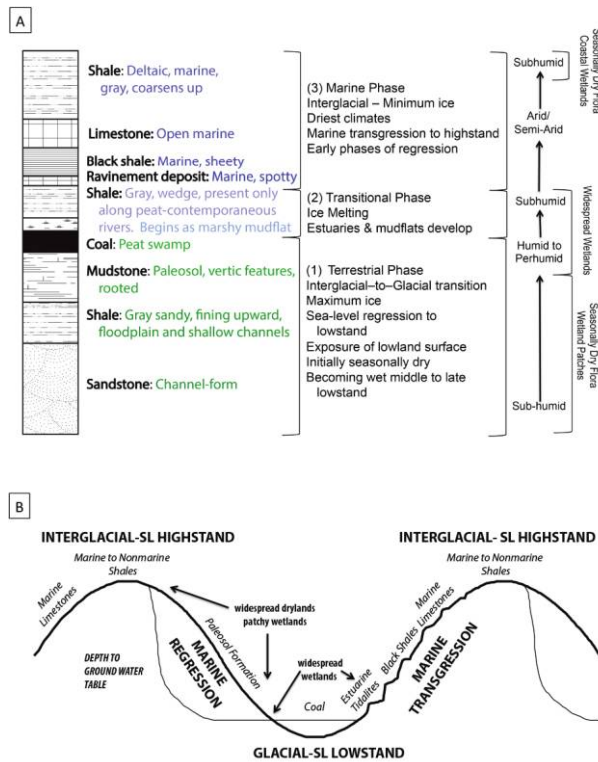
Fig. 3 Cyclothem as developed on the interior Pangean continental craton. *A*, Terrestrial and marine strata, with transitions between. Climate covaries with sea level (SL) change, both reflecting changes in ice volume. Vegetation reflects the prevailing climate. Dry-climate floras predominate from late sea level highstand to early to middle lowstand. Wetland floras predominate from middle to late lowstand into the early phases of transgression. *B*, Relationship between sea level, sedimentation, position of the terrestrial water table, and distribution of vegetation types. Note that sea level rise is marked by repeated meltwater pulses. Diagram modified from Rosenau et al. (2013*b*), with permission of the Society for Sedimentary Geology.

portion of Pangea based on dating with marine fossils, particularly condonts and fusilinids, and on radiometric methods (Heckel et al. 2007; Eros et al. 2012). Specific individual cyclothems have been traced from coal basins across large portions of the Euramerican continent into western Pangea, including paratropical regions (Ritter et al. 2002; Cecil et al. 2003*b*; Greb et al. 2003; Bishop et al. 2010). The ability to identify these cycles over a wide geographic expanse is an expectation realized, given that the controls are thought to represent global events.

Spatial variation in cyclothem expression. Classic mixed terrestrial and marine cyclothems (fig. 4) developed in North America mainly in low-gradient, flat cratonic settings where epicontinental seas alternated with coastal terrestrial fluvial-deltaic sedimentation (Watney et al. 1989). One or the other of these phases can predominate, depending on distance from the continental shelf. As Heckel (2008) has noted, cyclothems reflecting baseline 100,000-yr glacial-interglacial cycles are well represented in the American Midcontinent. Farther east, into the Eastern Interior (Illinois) and Appalachian Basins, ma-

rine incursions from the west were progressively less common, and both the number of cycles and the extent of marine influence diminished, resulting in fewer recognizably distinct 100,000-yr cycles. Larger 400,000-yr megacycles, into which the 100,000-yr cycles are grouped, are nearly always recognizable throughout the entire region (Heckel 2008; Belt et al. 2011; Falcon-Lang et al. 2011*a*).

Yet farther to the east, in central Pangea, the nature of glacial-interglacial cyclicity, on the finest scales, becomes increasingly difficult to recognize because of the complexity of the landscape in and around the Variscan portion of the Central Pangean Mountains and the overprint of syndepositional tectonics in some portions (Stollhofen et al. 1999; Opluštil 2005; Opluštil and Cleal 2007; Cleal et al. 2011). Even so, changes in climate and sedimentation patterns can be recognized to varying degrees in these areas and related to glacial-interglacial controls at various spatiotemporal scales (Oyarzun et al. 1999; Stollhoffen et al. 1999; Roscher and Schneider 2006; Bertier et al. 2008; Gastaldo et al. 2009; van Hoof et al. 2012; Opluštil et al. 2013*b*). Cycles of 10^5 yr are again recognizable in the Donets Basin of the Ukraine, in the eastern part of central Pangea, and can be correlated with those of the Midcontinent of North America (Eros et al. 2012).
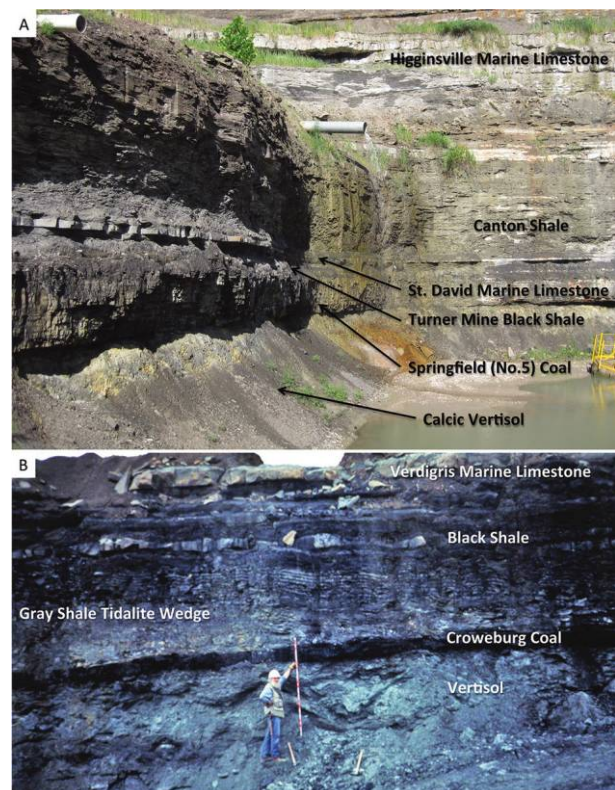

Fig. 4 Cyclothems in the field. Both late Middle Pennsylvanian (Desmoinesian) age. *A*, Springfield coal and associated rocks, Indiana. *B*, Croweburg coal and associated rocks, Kansas. Note in *B* the presence of a gray shale tidal sediments, part of an areally restricted wedge present only locally over the coal, in areas proximate to contemporaneous river channels, following conversion to estuaries during sea level rise. *B* courtesy of Blaine Cecil.

Drivers of cyclic sedimentation patterns. Although it is generally assumed that the proximate driver of cyclothem deposition was changing sea level, issues have been raised about the degree of sea level fluctuation that could be caused by the melting of continental ice in the Southern Hemisphere (Isbell et al. 2003*b*). Models of sea level fluctuation that call for 70–100 m of change within the average cyclothem, developed partly to account for the genesis of black shales (Heckel 1977, 1991*b*), have been challenged for many years (Zangerl and Richardson 1963; Coveney et al. 1991; Reischenbacher et al. 2013), and actual maximum water depths reached during interglacials may have been closer to 30 m (Isbell et al. 2003*b*). Further discussion of the origin of marine black shales is outside the scope of this review.

There is a considerable amount of discussion about the relationship between climate cycles and sea level cycles, as expressed in equatorial cyclothems. These have been studied recently through the lens of sequence stratigraphy (Gastaldo et al. 1993; Miller and West 1998; Catuneanu et al. 2009; Meyers and Milton 2011; Patzkowsky and Holland 2012), which, to paraphrase Catuneanu et al. (2009), is a method of describing different rock types, representing specific environments of deposition (facies), in terms of their stacking patterns in time and through space. These patterns will reflect changes in sea level, climate, and sedimentation, within the framework of the tectonic structure of a given depositional basin. It is uncontroversial to say that a mixed terrestrial-marine cyclothem represents the deposits formed during a single glacial-interglacial cycle. It reflects directional changes in sea level, linked mainly to fluctuation in the volume of glacial ice. If allowance is made for sufficient tectonically created space to bury these deposits in the long-term, so-called accommodation space, most of the elements of such a cycle will be preserved in the stratigraphic record. The correlation of individual cyclothems across large geographic areas, referred to above, suggests that accommodation space was produced continuously, on average, in the major basins.

During any such individual cycle, climate also changes systematically (Cecil et al. 1985, 2003*b*; Tandon and Gibling 1994; Olszewski and Patzkowsky 2003; Falcon-Lang 2004; Feldman et al. 2005; DiMichele et al. 2009*a*; Horton et al. 2012), strongly covarying with sea level changes. Within the pages of the articles cited above and others, however, the reader will find disagreement regarding the sea level position of key climate indicators, particularly paleosols (seasonally dry) and especially coals (wet with minimal seasonality): the principal points of contention regarding coals are that they formed during lowstand, during sea level rise and transgression, or at highstand, thus covering nearly all of the possibilities.

Tropical Cyclothems and Climate Cycles

In this article, I take the position that the weight of evidence, both empirical and from climate models, suggests that the most continuously wet (humid to perhumid climate) parts of Middle and Late Pennsylvanian glacial-interglacial cycles were to be found during mid- to late lowstand, at times of maximum glacial ice (Cecil et al. 2003*b*; Peyser and Poulsen 2008; Horton et al. 2010, 2012; Montañez and Poulsen 2013; fig. 3). Why is it important to establish this in an article ultimately focused on the spatiotemporal distribution of wetland and seasonally dry floras? In a description frequently attributed to the biogeographer Köppen (1936), plants are crystallized, visible climate. The spatial locations and dynamics of these various floras, as will be discussed below, have been and continue to be issues of some considerable controversy. Thus, it is crucially important, first, to document the evidence for strongly developed climate cycles and, second, to show that the kinds of beds in which plant fossils are found reflect those climates in a consistent and understandable way. From reading the conflicting views in the literature, one might think it is chaos out there. Instead, I would argue that these different interpretations can be reconciled, though I will not attempt to do so here. For consistency, I present a unitary viewpoint from the perspective of the principle of total evidence (Good 1967), the interpretation that provides the maximum fit of all the available data; I will attempt to justify each of the assertions made.

It is important to note that coal/peat is an indicator of rainfall. Extended periods of rainfall can raise local water tables to the surface quickly, on human timescales, as indicated by many extreme rainfall events in otherwise seasonally dry climates (Konrad 2001). It is very unlikely that, as is often asserted, the formation of peat swamps of vast extent and low mineral content was driven by rising sea level and coastal paludification. This is indicated strongly by the fact that there is little or no coal/peat in the highly seasonally dry to arid regions of western Pangea at exactly the same time such peat is present and widespread in the west-central and central Pangean coal basins, yet sea level rise and fall of a cyclothemic nature occurred in both places (Ritter et al. 2002; Bishop et al. 2010; Elrick and Scott 2010; Nelson et al. 2013*b*, 2013*c*). Hypothetically, peat can be present at any part of a sea level cycle—cyclothem—if a mechanism can be identified to make the climate sufficiently wet at that point in space and time (>10 mo a year with rainfall exceeding evapotranspiration in the tropics; Cecil and Dulong 2003). For example, most modern peat-forming environments similar to those of the Pennsylvanian are forming today, at or near sea level highstand, in tropical, high-rainfall environments, such as Sumatra (Anderson 1983; Cecil et al. 1985; Esterle and Ferm 1994). As modern analogues, peats forming in coastal lagoons or along shorelines in seasonal climates (e.g., Snuggedy Swamp of South Carolina [Staub and Cohen 1979], Changuinola peat of Panama [Cohen et al. 1989], Okefenokee Swamp of Georgia [Cohen 1984]) are not ideal analogues for most Pennsylvanian coals because they are (*a*) too high in mineral matter, so that after diagenesis and lithification they would yield organic-rich mudrocks rather than coals, and (*b*) too limited in areal extent to be comparable environmentally to Pennsylvanian coal beds, both in terms of their present-day extent and accounting for the entire extent and volume of the deposits that have formed from them over the past 10,000 yr.

A maximum glaciation, sea level lowstand position for most economic (low mineral matter content) coals is supported by a number of factors: sea level dynamics across an extremely flat depositional surface, subcoal paleosols indicative of a change from early rainfall seasonality to nearly continuous rainfall late in soil history, gradational contact between paleosols and overlying coals (histosols), and the presence of a marine transgression/ravinement erosional surface and sub-

sequently deposited marine rocks immediately above major coal beds. These factors are discussed in more detail below.

1. The Pennsylvanian craton was an extremely flat surface with gradients of perhaps only centimeters or kilometers over distances of thousands of kilometers (Watney et al. 1989). Thus, changes in the coverage of these surfaces by seawater, during both transgression and regression, were likely to have been rapid over great areal extents. This militates strongly against peat formation during transgression, particularly when it is considered that the ice-melting phase of an interglacial is much more rapid and pulse-like than the ice formation phase and thus accompanied by rapid sea level rises caused by melt-water pulses (for discussion of such effects during the Pennsylvanian, see Archer et al. 2014). In addition, changes in climate would have had effects over large areas due to the nearly uninterrupted nature of the flat topography.

2. During falling stages of sea level, when cratonic exposure would have occurred rapidly due to its flat aspect, and during early sea level lowstand, much of the cratonic surface was subject to pedogenesis (Joeckel 1994; Cecil et al. 2003b; Falcon-Lang et al. 2009). The soils (now paleosols) that formed during these intervals (figs. 4, 5) mark surfaces of nondeposition or limited deposition. They have characteristics that indicate climatic seasonality of varying degrees (Joeckel 1995, 1999; Feldman et al. 2005; Catena and Hembree 2012; Rosenau et al. 2013a, 2013b). These empirical observations also suggest seasonally dry climates during the falling stages of sea level and during the early phases of lowstand (fig. 5). Climate models independently predict strongly seasonal equatorial-Pangean climates in these same phases of a sea level sequence (Horton et al. 2012).

3. The paleosols formed during regression and early lowstand show evidence of changing climatic conditions during their formation (i.e., they are polygenetic). Almost without exception, they vary from indicative of seasonal dryness in their formative stages to indicative of increasing moisture input under humid climate during their later stages. It was during the latter phases that various clays and minerals, including iron, were translocated down the soil profile, resulting in gleying, indicating both that the soil was still well drained and that weakly acidic conditions, resulting from organic matter accumulation, had begun (converting low-solubility ferric to more soluble ferrous iron; Miller and West 1993; Miller et al. 1996; Tabor and Montañez 2004; Driese and Ober 2005; Rosenau et al. 2013a; fig. 5). Subcoal paleosols frequently transition to coal beds, indicating that water tables rose to the surface of the soil, most likely driven by increased rainfall, which suppressed decay and permitted the accumulation of organic matter (Cecil et al. 2003b; Rosenau et al. 2013a, 2013b). It is unlikely that rising sea level would cause a rise in base level of sufficient geographic extent, i.e., across most of the vast Pangean interior continental shelves, to initiate peat formation simultaneously across the region (see point 4; coals are not notably time transgressive), nor can rising sea level account for late-stage soil gleying because it provides no mechanism to translocate soluble iron downprofile or out of the soil entirely.

4. Where it has been possible to determine it, Pennsylvanian coal beds appear to represent peat bodies that were contemporaneous throughout their distributions (this is true whether they formed as one temporally unbroken swamp or as several stacked peat bodies separated by hiatuses; Jerrett et al. 2011). That is, they are not directionally time-transgressive deposits, significantly older at the shelf edge and progressively younger inland; they did not form in narrow coastal bands being pushed continuously inland by rising sea level ahead of other narrow bands of marine muds and limestones. This time equivalence is indicated by such features as ash-fall partings in several coal beds: the Fire Clay coal of the Southern Appalachian Basin (Lyons et al. 1992; Greb et al. 1999b), several coals in the mid-Pennsylvanian of the Czech Republic (Opluštil et al. 2007), and a Pennsylvanian-Permian coal from the Wuda District in China (Pfefferkorn and Wang 2007; Wang et al. 2012). Also indicative of widespread age synchrony are mineral partings continuously recognizable throughout coal beds: the "binder" beds, which separate petrographically and palynologically distinct benches of the Pittsburgh coal of the Central Appalachian Basin (Gresley 1894; Eble et al. 2006), or by the blue band of the Herrin coal of the Illinois Basin, which may carry into equivalent coal beds in the Midcontinent (Greb et al. 2003).

5. At this point, it is important to remember that most Pennsylvanian coals formed as histosols, which are organic-rich soils. Thus, they reflect very specific kinds of climatic conditions (humid to perhumid, in the tropics, by analogy with modern tropical peats; Anderson 1983; Cecil and Dulong 2003) and formed in situ. In the case of Pennsylvanian-age economic coal beds, the parent peats were quite low in mineral matter; otherwise, following diagenesis they would have formed organic-rich shales rather than coals. Thus, peat swamps either were protected from mineral matter input or formed during times when mineral matter transport was limited. Under conditions suitable for tropical peat formation, rainfall exceeds evapotranspiration and runoff nearly year-round (humid to perhumid climates; Cecil and Dulong 2003). Under such conditions, plant density on the land surface is high throughout a drainage basin, regardless of elevation, as is subsequent rooting, which binds sediment and limits the entry of mineral matter into stream and river drainages, including those beyond the limits of peat formation (Cecil et al. 1993, 2003a).

6. Major coals of middle and late Pennsylvanian age from American coal basins are overlain by a surface formed by marine transgression, known as a ravinement surface because of its erosional base (Demaris et al. 1983; Demko and Gastaldo 1996; Liu and Gastaldo 1992; DeMaris 2000). Immediately above this surface may be shell hash or thin limestones of marine origin. More generally, however, the ravinement surface is overlain by thin, marine, sheety, black shale, which is overlain by open marine limestone (fig. 4). Under such circumstances, the coal must have formed prior to transgression, with flooding of the craton by marine water. Such coals are difficult to place at highstand, given they are overlain by open marine deposits, often of considerable thickness.

Recent climate models, both conceptual (Cecil et al. 2003b) and numerical (Peyser and Poulsen 2008; Horton et al. 2010, 2012), suggest that in the tropics of Pangea, glacial maxima/sea level lowstands were the wettest parts of glacial interglacial cycles, varying regionally in amount. Furthermore, they suggest that during interglacials there were no large, ever-wet areas

Fig. 5 Coals (paleohistosols) and underlying paleovertisols, illustrating climatic contrasts and transitions between these two types of soil deposits. Paleosols indicated by double-headed arrows. Coals labeled with letters. *A*, Cohn coal (CC), Late Pennsylvanian (Missourian), Illinois. *B*, Harlan coal (HC), Late Pennsylvanian (Missourian), West Virginia. AMZ = Ames Marine Zone, the last major marine transgression of the late Paleozoic documented in the Appalachian basin. Note two paleosols, both vertisols with calcic horizons and, in 2, calcified root casts. *C*, Danville (No. 7) coal (D7C), Middle Pennsylvanian (Desmoinesian), Indiana. Paleosol shows iron staining demonstrating incomplete gleying and clear horizonation. *D*, Unnamed Staunton Formation coal (USFC), Middle Pennsylvanian (Desmoinsian), Indiana. Note strong expression of vertical slickensided surfaces in the paleosol. *E*, Herrin (No. 6) coal (H6C), Middle Pennsylvanian (Desmoinesian), Indiana. In this location, the Herrin coal is very near the edge of its development and is only a few centimeters thick. It is underlain by a vertic paleosol with calcium carbonate nodules. *F*, Core through paleosol below the Herrin (No. 6) coal, Indiana. Core segments are 61 cm long. Note strong gleying at the top of the soil profile, indicative of late-phase high levels of soil moisture. This is superimposed on earlier phases of soil development that indicate much seasonally drier climatic conditions, including nodular calcium carbonate, at ~90-cm depth at white bracket and angular vertic surfaces throughout the upper 2 m of the profile. Near base of profile, at arrowhead, on left, the soil is red.

for coal swamp and other wetland vegetation to migrate to. Horton et al. (2012) did find evidence of high volumes of strongly seasonally distributed rainfall during the early parts of interglacials and into early highstand. In combination with highstand deltaic sedimentation (much like that found around the world today; Stanley and Warne 1994), this may help account for possible highstand coals. Such coals are rarely of more than very local economic thickness and quality (low ash and sulfur) and lack the subcoal paleosols indicative of strong climate contrasts. These features are consistent with their formation in localized wet habitats or under rainfall conditions less than ideal for peat preservation and as intrinsic elements in coastal settings, such as highstand to regressive-phase deltas.

On longer timescales, at coarser levels of resolution, decreases in ice volume and increases in global sea level are correlated with increased seasonality of rainfall (Tabor et al. 2002; Poulsen et al. 2007; Tabor and Poulsen 2008). These patterns of change in climate and ice volume appear to be strongly correlated with and probably driven by changes in atmospheric CO_2 concentration (Montañez and Poulsen 2013). Furthermore, there is evidence that the Pennsylvanian tropics at times, or perhaps at parts of glacial-interglacial cycles, may have been cooler than those of the modern world (Soreghan et al. 2008; Tabor et al. 2013a). These findings are in conformance with the surmise of Fredericksen (1972) that Pennsylvanian wetlands may have been cooler than generally envisioned.

Late Paleozoic Ice Age–Quaternary Conflicts

It is important to acknowledge that there are conflicts between the interpretation presented here—that is, that it was wettest in the equatorial regions of Pangea during glacial maxima through late glacial stages and driest during interglacials through early glacial phases—and the patterns found in the equatorial regions of the Pleistocene through Recent tropics. This is a subject that would require considerably more space to discuss than is possible here. Several things should be considered, however. In the present ice age, there has been a great deal of ice in the north-polar region. There is only limited evidence for high-latitude northern ice in the LPIA. This alone would cause major differences in patterns of atmospheric circulation (Müller et al. 2013). Continental configurations are quite different in the two ice ages as well: today's dispersed, high-aspect, continental configuration differs greatly from the huge Pangean supercontinent, with its nearly E-W transequatorial mountain range and vast areas of low-elevation, flat, interior continental shelves.

Finally, there are important differences in the plant composition of the two time periods that may have important consequences for the tropical hydrological cycle. The presence of angiosperms is the great and notable difference, and studies by Boyce and colleagues (Boyce et al. 2009, 2010; Boyce and Lee 2010; Lee and Boyce 2010) suggest that angiosperms can translocate water at rates up to 10 times greater than any other group of vascular plants. To the extent that these determinations are correct, the angiosperms, as one of the above-cited titles indicates, "put the rain in the rainforest." The high rates of evapotranspirative moisture released by angiosperm trees create the high volume of recycled water that makes current interglacial rainforests wet. The implication is that if these

forests were composed of any other groups of plants (such as lycopsids, marattialean tree ferns, and pteridosperms), there would be insufficient evapotranspiration to create this rainfall feedback. Instead, late Paleozoic wetlands would have to be made wet by primary, atmospheric-circulation-driven rainfall. Thus, models that wish to reconstruct late Paleozoic wetlands must not assume landscapes populated by plants with angiosperm-type physiologies and the associated recycling of water.

Pennsylvanian Lowland Vegetation

There were two principle species pools, or biomes, that alternately dominated the Pennsylvanian lowlands, plus some subsidiary floras that may have been edaphic specialists. The better known of these floras was composed of plants that were obligately tied to wet substrates and possibly to high levels of atmospheric humidity (Scott 1977; Gastaldo 1987; Hilton and Cleal 2007; Galtier 2008; King et al. 2011; Wagner and Castro 2011; see summaries in Eble and Grady 1990; DiMichele and Phillips 1994). The other flora consisted of plants that were tolerant of moisture deficits of varying degrees (Leary and Pfefferkorn 1977; Galtier et al. 1992; Falcon-Lang et al. 2009; Plotnick et al. 2009; Bashforth et al. 2014). These floras oscillated in dominance through time on glacial-interglacial temporal scales (Falcon-Lang 2003c, 2004; Falcon-Lang and DiMichele 2010), reflecting the climatic variations that occurred in concert with glacial-interglacial cycles and their global effects on climate, sea level, and other factors.

Each major species pool can be subdivided further spatially. Under humid climates, for example, there is a distinct segregation in the dominance patterns and compositional aspects of floras from peat substrate swamps, mineral substrate swamps, and terra firma mineral soils. Within any of these species subpools, distinct, if often gradational, communities can be recognized, reflecting the combined effects of local environmental conditions, dispersal limitation, and incumbency/competition. Similarly, the species pool of seasonally dry climates consisted of a number of compositionally overlapping assemblages. These differ both quantitatively and qualitatively with regard to the dominant elements, which presumably reflects the duration of moisture deficits but also the effects of various biotic factors and smaller-scale physical conditions.

In addition to spatial complexity, there are temporal patterns of change in these distinct species pools. For the most part, these changes, at the level of species and generic composition, occurred gradually over time, driven by evolutionary change (within ecological context). At times, however, the changes in species pool composition were extensive and appear to have occurred rapidly, at rates and to degrees that suggest large-scale regime shifts (Phillips et al. 1974; DiMichele et al. 2009a). Such changes are more common among wetland floras than within the group of seasonally dry floras, for reasons discussed below.

A note must be made here on the matter of diversity, which will be addressed later as well. Based on modern tropical analogues (Gentry 1982; Valencia et al. 1994; Condit et al. 1996, 2002, 2005; Wright 2002; Hubbell et al. 2008; Lamarre et al. 2012), habitat quality is higher in terra firma lowland environments than in swamps (Prance 1979, 1989; Terborgh et al. 2002, fig. 1.2; Koponen et al. 2004; Lopez and Kursar 2007).

That is, they have higher nutrient availability, better oxygenation of soils, and lower levels of physical stress. Consequently, terra firma settings are usually of higher diversity, often considerably higher than swamps in the same region, under almost any climate regime as wet as or wetter than semiarid. It therefore seems a legitimate starting hypothesis to expect terra firma lowland humid-climate environments to have been more diverse than swamps during the Pennsylvanian. Studies of Pennsylvanian floras, however, as described below, suggest that any such differences at that time were sufficiently muted as to be nearly indetectable, compared to the modern (and, almost certainly, the post–Late Cretaceous) world. There appear to have been large differences in diversity between humid-climate terra firma floras and tropical dry floras of the Pennsylvanian. Seasonally dry floras are not nearly as well known and characterized as wetland assemblages (for preservational reasons), which limits comparison to a somewhat anecdotal level. But comparisons of local floras, made for paleoecological or stratigraphic studies (Gastaldo et al. 2004; Libertín et al. 2009; Bashforth et al. 2010, 2011, 2014; King et al. 2011; Cleal et al. 2012; van Hoof et al. 2012), suggest that floras of humid climates were much richer in species and genera, and even in the numbers of higher-taxonomic evolutionary lineages represented, than were seasonally dry floras under subhumid to semiarid climate regimes.

Wetland Floral Composition

The Pennsylvanian tropical wetland flora is possibly the best-known fossil flora of the pre-Quaternary. Thus, this review need only be brief. Descriptions of the macroflora, both compression-impression and anatomically preserved, can be found in numerous publications dating to the early 1800s, when formal paleobotanical taxonomic nomenclature was established (von Sternberg 1820). The palynoflora is equally well known, primarily from studies of coal and associated rocks (Peppers 1996). There were two major species pools that comprised this flora, and these succeeded each other in time. From the late Mississippian to the end of the Middle Pennsylvanian, peat-forming swamps were heavily populated by lycopsids and pteridosperms, with cordaitaleans as significant elements at times. Other, mineral soil, wetlands were dominated by pteridosperms and sphenopsids with lycopsids in less abundance. Beginning in the late Middle Pennsylvanian, tree ferns began to increase in abundance (Pfefferkorn and Thomson 1982) in all types of wetland environments (figs. 2, 6A). Near the Middle–Late Pennsylvanian boundary, there was a major floristic turnover (Phillips et al. 1974; Falcon-Lang et al. 2011a), with tree ferns becoming the dominant elements in peat-forming swamps and codominants in many other wetland settings (figs. 2, 6B). The timing of this turnover varied slightly across Euramerica (Cleal et al. 2009; Wagner and Álvarez-Vázquez 2010), but the results, in terms of dominance-diversity patterns, were the same everywhere. Many of the lineages, including some of the lycopsids, dominant in Middle Pennsylvanian assemblages, survived well into the Permian in Cathaysia (Hilton and Cleal 2007), representing a species pool from which dispersal back into Euramerica seemingly did not occur. Figures 7 and 8 represent a compilation of examples of the Pennsylvanian wetland plants from major American coal
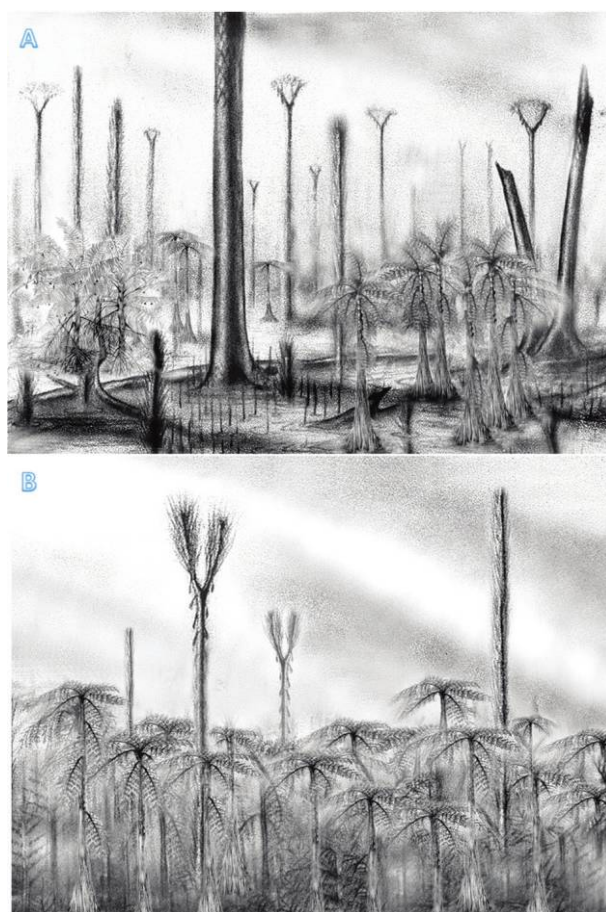

Fig. 6 Reconstructions of two coal swamps. *A*, Middle Pennsylvanian swamp dominated by lycopsids (*Lepidophloios*), tree ferns, and pteridosperms, with open architecture, lacking a closed canopy. *B*, Late Pennsylvanian swamp dominated by tree ferns, which form a nearly closed canopy, and emergent lycopsid trees (*Sigillaria*), with pteridosperms in the understory. Reconstructions by Mary Parrish, Smithsonian Institution. Reprinted from DiMichele et al. (2009a).

basins. These are field photographs of specimens, primarily from underground and surface coal mine exposures, which hopefully will provide somewhat more context than more refined photos of selected specimens.

Pennsylvanian tropical floras of all habitats were significantly less diverse than modern tropical rainforests. A comparison of Cretaceous-Tertiary and Pennsylvanian-Permian paleobotanical samples, drawn from single excavations of ~1 m² and 1/2 m deep (Wing and DiMichele 1995), revealed no significant differences at that scale, which modern studies suggest samples ~0.1–0.5 ha of standing vegetation (Burnham 1993). Most samples comprised around 10 species. However, when transects made laterally within single beds were compared, the younger angiosperm-rich assemblages proved to be much more diverse than those of the Paleozoic, indicating an intrinsic difference in landscape-level diversity, reflected in global species diversity compilations (Niklas et al. 1980). At larger spatial scales, the most diverse Pennsylvanian flora from one instant in time is the Mazon Creek flora, of late Middle Pennsylvanian
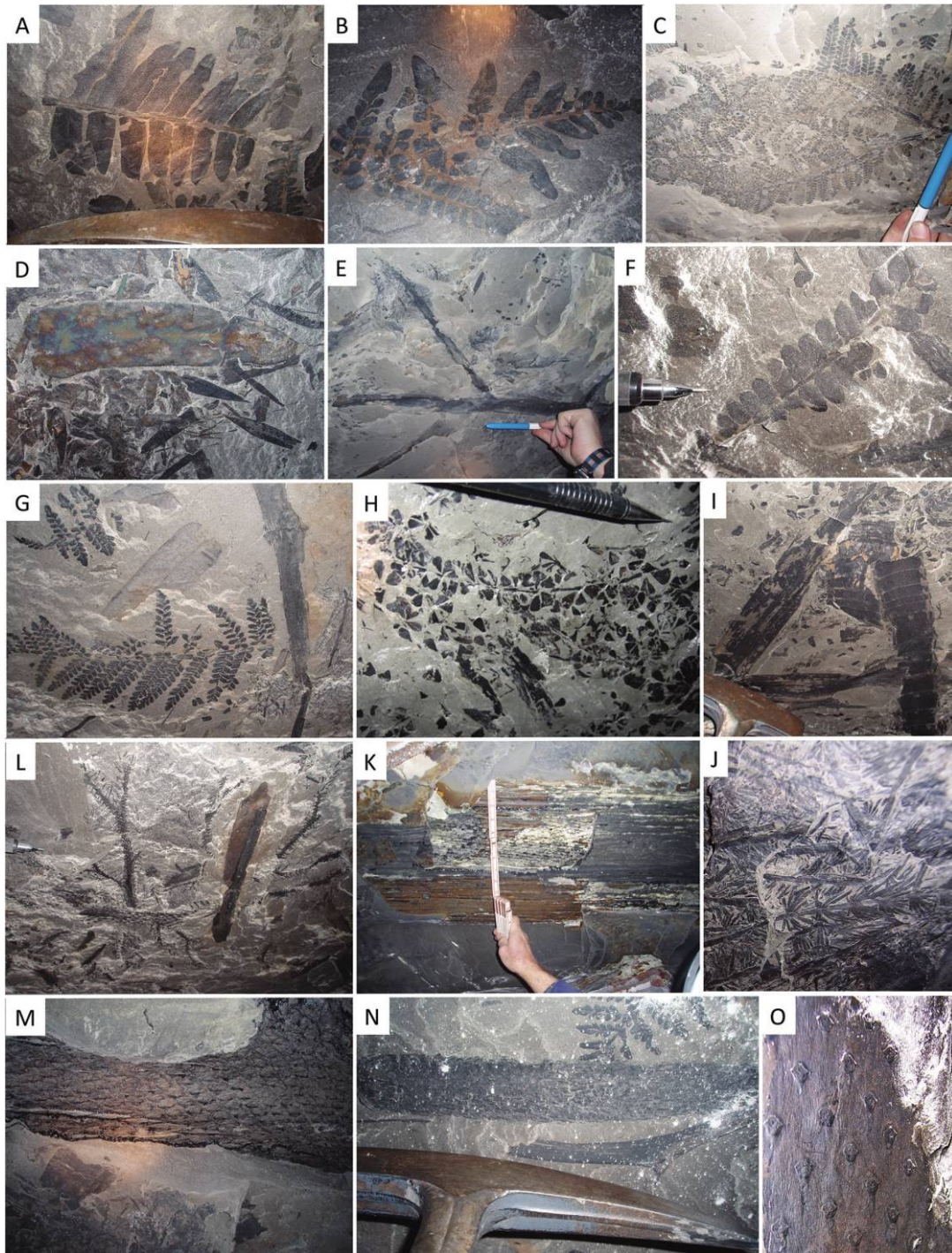
Fig. 7 Wetland plants from the roof shales of the Springfield (No. 5) and Herrin (No. 6) coals of the Illinois Basin. All photos were taken in-mine, in areas where the coal had been removed, exposing the overlying shales. The author apologizes for the lack of scales in some photos; in many cases specimens were out of reach in the coal roof, precluding inclusion of a scale. *A*, *Neuropteris flexuosa*; pteridosperm foliage. *B*, *Neuropteris flexuosa*; pteridosperm foliage. *C*, *Laveineopteris rarinervis*; pteridosperm foliage. *D*, *Macroneuropteris scheuchzeri*; pteridosperm foliage (single pinnule of much larger compound leaf). *E*, Pteridosperm stem with petioles of leaves still in attachment. *F*, *Odontopteris* sp.; pteridosperm foliage. *G*, *Pecopteris* sp.; tree fern foliage. *H*, *Sphenophyllum emarginatum*; ground cover sphenopsid. *I*, *Calamites* stems; sphenopsids. Note characteristic jointing of stem. *J*, *Asterophyllites equisetiformis*; calamitealean foliage. *K*, *Lepidodendron* fallen main trunk; a giant lycopsid tree. Scale in feet and tens of feet. *L*, *Synchysidendron* lateral branches; deciduous lateral branch axes of a large lycopsid tree, with attached leaves. *M*, *Lepidodendron* sp.; branched axis from crown of this large lepidodendrid lycopsid. *N*, *Lepidostrobus*; cone of a large lepidodendrid tree. *O*, *Asolanus camptotaenia*; bark of moderate-sized lepidodendrid tree.
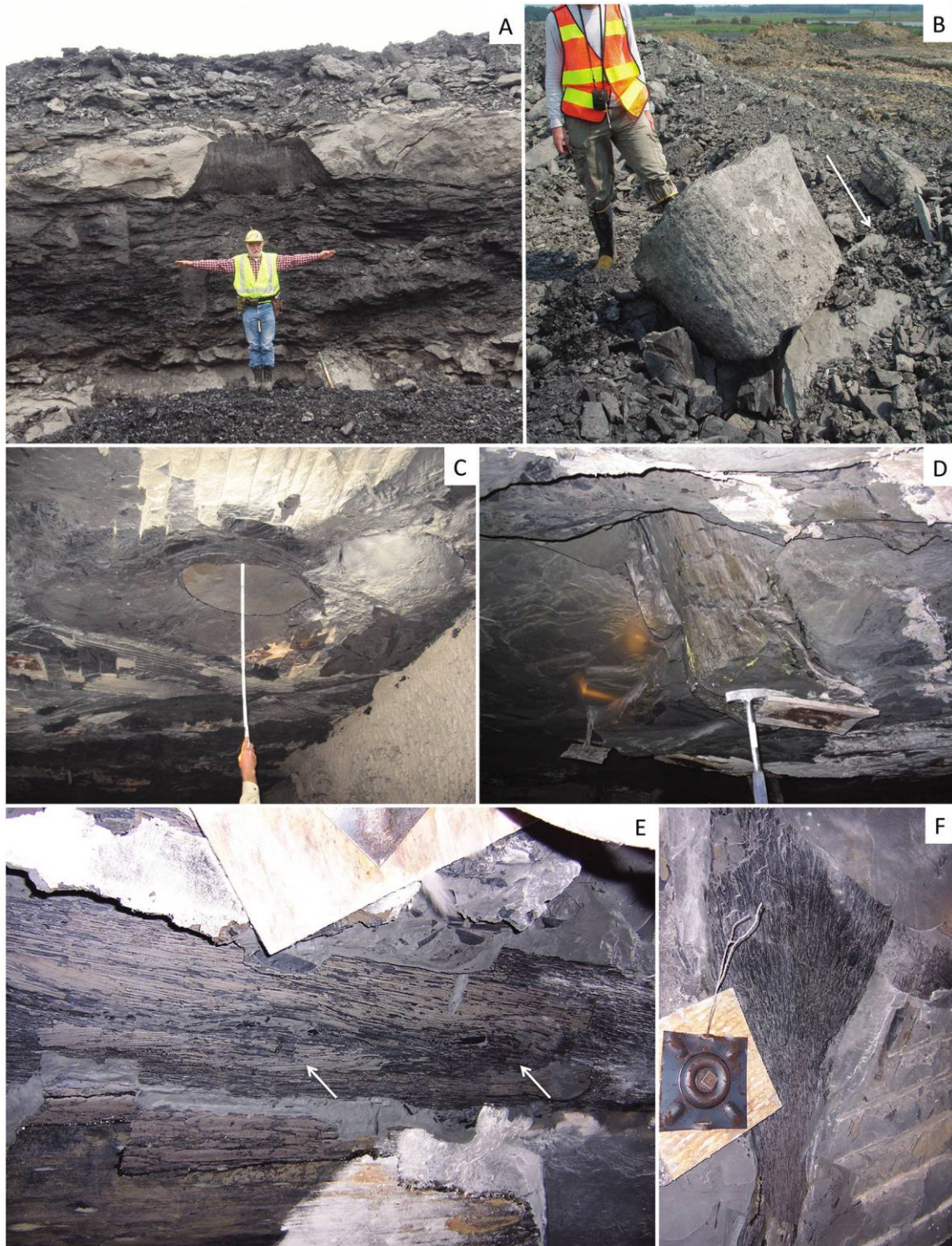
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Fig. 8 Wetland trees, field photographs. All are from roof shales of Middle Pennsylvanian (Desmoinesian)–age coals. *A*, Large *Sigillaria* stump cast above thin coaly layer. *B*, Exhumed *Sigillaria* tree stump. *C*, Base of identified lycopsid tree buried in the roof shale, a feature colloquially known as a kettle bottom. *D*, Tree trunk of lycopsid partially exposed in roof shale by small roof fall. *E*, Prostrate trunk of a marattialean tree fern. Arrows point to scars left following leaf abscission. Longitudinal striations are adventitious roots of the root mantle. Metal roof bolt at top of photograph is 15.25 cm on a side. *F*, Terminal portion of a *Cordaites* crown branch bearing a tuft of long grasslike *Poacordaites* leaves. Metal roof bolt for scale.

age (Wittry 2006). This flora is drawn from an entire drainage basin, including coastal, inland swamp, and low-elevation wet soil habitats, and is compositionally conservative, having been identified across a distance of >1000 km (Moore et al. 2014); when accounting is made for taxonomic uncertainties, synonymy, and multiple names for organs of the same plant, a reasonable estimate of diversity appears to be ~100 species (Pfefferkorn 1979). A broader study of European basins (Cleal et al. 2012) concluded that Pennsylvanian wetland landscapes harbored 40–100 species at any point in space and time, reaching perhaps 120 species at the regional level of >10^5 km², but that there was no significant difference in species diversity between modern flooded coastal swamps and Pennsylvanian wetlands in general (not just swamps). This latter finding is particularly significant. It partially reflects the strong physical selective factors that swamp habitats present (and the Pennsylvanian lowlands harbored vast swamps compared to the modern tropics), which lead to strong ecotonal boundaries between swamps and surrounding terra firma habitats, even if the prevailing climate is humid. Such swamp boundary ecotones are asymmetrical (DiMichele et al. 1987) in the sense that wetland plants do not compete well with terra firma–centered species, restricting the former to the semiflooded sites they can tolerate. In contrast, the terra firma species cannot grow under flooded conditions and so are excluded from these habitats. Nonetheless, the Cleal et al. (2012) study includes floras drawn from more than swamp settings, suggesting that the Pennsylvanian humid-climate lowlands were, in general, much lower in diversity than those of equivalent environments in the modern world.

The dominant plant groups in wetlands comprise four distinct evolutionary lineages: lycopsids, ferns and sphenopsids, all free-sporing heterosporous or homosporous plants, and seed-producing plants of several types. This means that all the known major body plan groups of plants extant at that time were dominant players in wetland ecosystems (DiMichele and Phillips 1996a). The Paleozoic pattern is notably different from that of today, where seed plants and, in some instances, ferns are the principal significant elements of wetland floras (Cronk and Fennessy 2001) and of nearly all terrestrial ecosystems (Bond 1989).

The principal lycopsids were several genera of trees most closely related to the modern qullworts (*Isoetes* and *Stylites*; Bateman 1994), including such recognizable names as *Lepidodendron* and *Sigillaria*, but also many others, such as *Paralycopodites*, *Bergeria*, *Diaphorodendron*, *Synchysidendron*, *Hizemodendron*, *Lepidophloios*, *Sublepidophloios*, and *Omphalophloios* (Wagner 1989; Bateman et al. 1992; Opluštil et al. 2010; Thomas et al. 2013; DiMichele et al. 2013a; Álvarez-Vázquez and Wagner, forthcoming). These trees, supported by a cylinder of bark rather than a core of wood, are among the most unusual in all of earth history (Andrews and Murdy 1958). Some of the larger species reached heights of more than 30 m (Thomas and Watson 1976), whereas others were of more modest size. The trees comprised three dominant growth architectures (Bateman et al. 1992; DiMichele et al. 2013a): those that grew as unbranched poles, producing cones periodically on short, trunk-borne peduncles (mainly *Sigillaria*); those of monocarpic habit, in which a dichotomously branched crown, bearing the reproductive organs, was produced only

in the final phases of growth (primarily Lepidodendraceae; fig. 9A, *left*); and those that produced deciduous lateral branches on the trunk and in the final-phase crown, thus throughout the life of the tree (the ancestral condition found in several families; fig. 9A, *right*). With rare exceptions, these plants were confined to soils with high moisture content and, most likely, standing water throughout much of the year (DiMichele and Phillips 1985), a role for which they had numerous morphological adaptations (Phillips and DiMichele 1992) and specialized physiologies (Green 2010). In peat-forming environments, most lycopsid trees were abundant to dominant in the wetter parts of swamps with periodic standing water, so-called rheotrophic swamps, but others may have been centered in
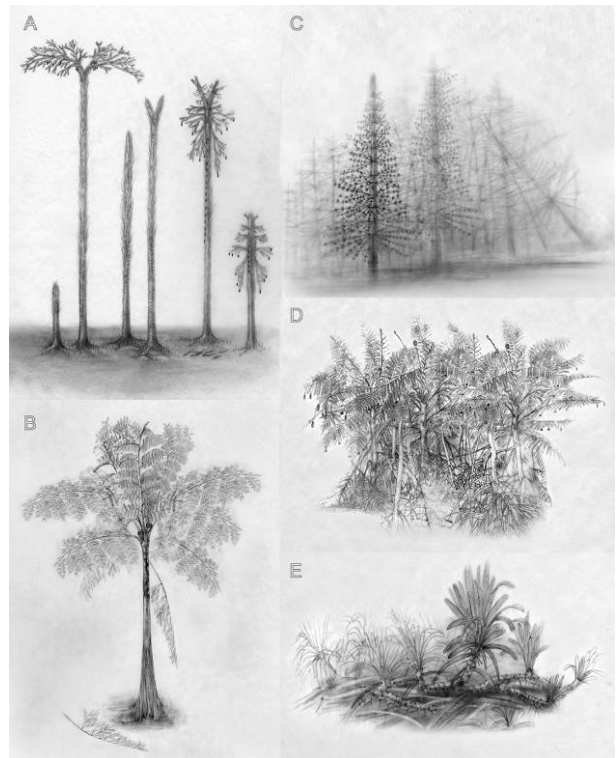

Fig. 9 Wetland plants reconstructed. *A*, Two growth forms of lepidodendrid lycopsids, plus immature stages. The four trees to the left are growth stages of forms with a monocarpic crown (present only in the final reproductive phases of growth), typical of the Lepidodendraceae (*Lepidodendron* or *Lepidophloios*). To right is a pair of polycarpic trees; these produced cones on deciduous lateral branches, giving them an extended period of reproduction, which begins as soon as lateral branch production is initiated. These branches were shed from the tree following maturation of the strobili, which must have created a large litter field. *B*, Marattialean tree fern, *Psaronius*. Note large fronds and thick mantle of adventitious roots, which provide both support and water transport to the crown. *C*, *Calamites* of a small form with limited wood development. Notable features are its rhizomatous growth habit, leading to dense stands of plants, and its whorled organization of appendicular organs. *D*, Medullosan pteridosperms, reconstructed as a dense stand that gain support from leaning on one another. Large seeds are borne in the fronds. *E*, Small, scrambling cordaitalean of the *Cordaixylon* type. Reconstructions by Mary Parrish, Smithsonian Institution.

highly nutrient-depleted, highly oligotrophic parts of raised or ombrotrophic swamps. Regardless of habitat preference, all genera appear to have been widespread across the Euramerican part of Pangea in the Pennsylvanian (Thomas 2007), and many extended into the Cathaysian portions of Pangea during the Permian (Hilton and Cleal 2007; Wang et al. 2009).

Wetland ferns fall into two broad groups based on their growth form: the scrambling, climbing, ground cover forms (Phillips 1974) and the tree forms (Morgan 1959). The low-growing forms and vines comprise the zygopterid (Phillips and Galtier 2005) and filicalean (Brousmiche 1983; Rothwell 1987; Phillips and Galtier 2011) ferns and were widespread in wetlands (DiMichele and Phillips 2002). The dominant Euramerican Pennsylvanian-age tree ferns were primarily the Marattiales (fig. 9B), but tree forms also existed in other evolutionary lineages of ferns (Sahni 1929; Pfefferkorn 1976). The Marattiales are a group that is still extant today and of primarily tropical distribution. In this diverse group (Lesnikowska 1989; Millay 1997; Liu et al. 2000; He et al. 2013), the stems (*Psaronius*, *Caulopteris*, *Megaphyton*) were supported by a mantle of adventitious roots (Ehret and Phillips 1977). The root mantle hosted a large array of climbing and epiphytic plants (Rößler 2000), making *Psaronius* an important ecosystem engineer. In addition, the adventitious roots, and in some species the stems also, were composed mainly of air spaces, creating inexpensive trees, from the viewpoint of carbon allocated to structure (Baker and DiMichele 1997). Cheap construction was accompanied by large fronds, probably borne in an umbrella-form crown, on which were produced vast numbers of reproductive organs and prodigious numbers of spores. The dispensability and large numbers of these spores permitted the marattialean ferns to locate and colonize remote, often isolated areas of wet substrate, allowing them to persist in areas varying from large swamps to small, isolated wet areas embedded within seasonally dry landscapes, well into the drier parts of Permian Pangea (DiMichele et al. 2006b).

The sphenopsids are composed of two large taxonomic groups that have different growth architectures and ecologies. The sphenophylls were small, scrambling, thicket-forming, and climbing plants (Batenburg 1982; Galtier and Daviero 1999; Bashforth and Zodrow 2007) that colonized exposed substrates under generally wet climatic regimes. The more widespread group was the calamitaleans, close relatives of the extant Equisetales (fig. 9C), a group that likely includes considerably more taxonomic, structural, and ecological diversity than is understood at present (Rößler and Noll 2006). These plants are widely known from stem casts preserved in upright position but also as compressed stems, often in streamside and lakeside habitats (for a large review of literature see DiMichele and Falcon-Lang 2012). They also are well documented from petrified material in coal-swamp settings (Andrews and Agashe 1965; Spatz et al. 1998) and clastic wetlands (Rößler and Noll 2006; Mencl et al. 2013), from which stem sizes are often considerably larger than those known from compression preservation. Most calamitaleans were rhizomatous, the only group of ecologically dominant, large-size wetland plants with this habit, which enabled them to persist through or recover from repeated inundation by flood-borne sediments (Gastaldo 1992; DiMichele et al. 2009b). The strong ties of these plants to riparian corridors also permitted them,

like the marattialean ferns, to locate and persist in wet areas of otherwise seasonally dry environments (Falcon-Lang 2003b). Wetland seed plants consisted of several distinct evolutionary lineages with markedly different architectures. The principal groups were the pteridosperms Medullosales, Lyginopteridales, and Callistophytales and the conifer sister group Cordaitales.

From a biomass perspective, the most important of the pteridosperms were the medullosans, a group that has received, perhaps, more attention from paleobotanists than any other group of Pennsylvanian plants—thus, there is a large literature that is altogether taxonomic, morphologic, floristic, and biostratigraphic. A highly diverse and ecologically differentiated group of plants based on studies of compression foliage, they also comprise a variety of growth architectures, including lianas and small trees (fig. 9D) of various configurations (Pfefferkorn et al. 1984; Dunn et al. 2003; DiMichele et al. 2006a), a great many of which were likely ground cover or subcanopy plants (Wilson and Fischer 2011; Raymond et al. 2013). Found in both clastic and peat substrates (Cleal and Shute 2012), much greater diversity has been described in the former, and no species have yet been described that are specific to peat substrates. Biogeographic differentiation has been documented in the Variscan mountain region of Euramerica (Cleal 2008b), and the group shows little dispersal into eastern Pangea during the Permian, even though wetlands persisted there after disappearing in central and western Pangea (Hilton and Cleal 2007). Thus, although tied to wetlands, possibly the higher nutrient parts thereof, the medullosans seemingly did not have the ability to colonize drier habitats or were limited in dispersal ability. The lyginopterids comprise several genera of small woody plants, including liana and thicket-forming and scrambling habits, typified by various morphological climbing aids (Krings et al. 2003), and may have formed a significant component of the ground cover in many parts of the wetland habitat (Wilson and Fischer 2011; Tenchov 2012). They are common, diverse, and widespread, known from both mineral substrates and peat swamps, particularly in the Early and Middle Pennsylvanian, declining in the Late Pennsylvanian (Cleal 2008a). The callistophytaleans were a highly derived group of pteridosperms (Rothwell 1981) that were widespread throughout the Middle and Late Pennsylvanian. They were primarily ground cover with scrambling habits or possibly lianas (Galtier and Béthoux 2002). Of evolutionary significance, possibly ancestral to more derived seed plants, they were a minor component of floras in both mineral and peat substrate wetlands.

The cordaitalean gymnosperms were the other major group of seed plants in Pennsylvanian wetlands (Costanza 1985; Trivett and Rothwell 1988; Trivett 1992). Sister group to the conifers, the cordaitaleans were taxonomically diverse, ranged in size and habit from small scrambling forms to large forest trees, and occurred throughout a large range of habitats, perhaps larger than any other group of tropical plants, ranging from wetlands (Greb et al. 1999a; Falcon-Lang 2005; Šimůnek 2008; Raymond et al. 2010) to well-drained settings or seasonally dry habitats of many different kinds (Falcon-Lang and Scott 2000; Falcon-Lang et al. 2011b, 2011c). In wetland habitats, the group is most often portrayed as mangroves, based on an interpretation of root morphology presented in an influential article (Cridland 1964). Recent analyses, however,
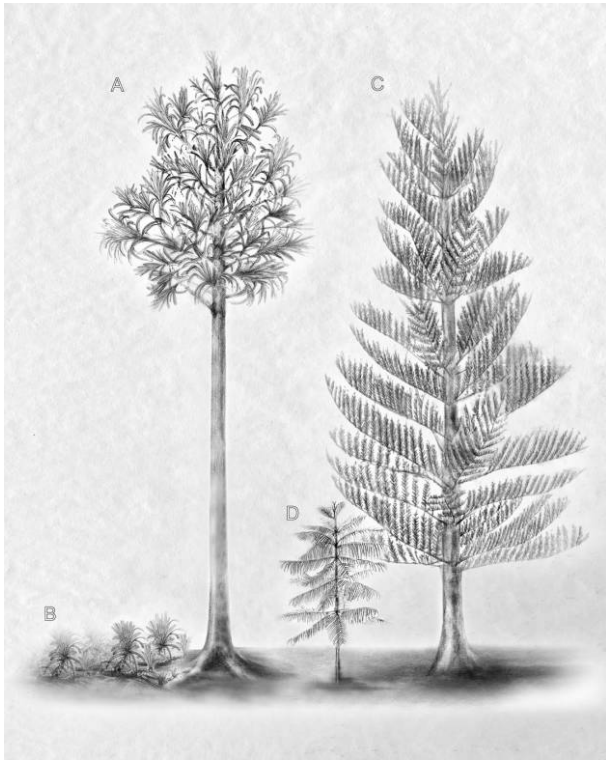
Fig. 10 Dryland plants reconstructed. *A*, Large cordaitalean tree with crown of large strap-shaped leaves. These trees may have exceeded 50 m in height. Note smaller scrambling form (*B*), for size comparison. *C*, Walchian conifer of large stature, characterized by plagotropic branching. *D*, Walchian conifer of small stature. This may have been the size of mature adult plants at some periods in the history of these plants; at other times, this size would have been characteristic of a juvenile (modified from Hernandez-Castillo et al. 2003). Reconstructions by Mary Parrish, Smithsonian Institution.

have questioned this hypothesis (Raymond et al. 2010), and a stilt-rooted *Rhizophora*-mangrove-like growth habit seems not empirically supportable. Recent cuticular analyses (Šimůnek and Florjan 2013) suggest that the species known from peat-forming wetlands were distinct from those found in seasonally dry habitats. Diversity in the group is not well understood, however, because of the fragmentary preservation and limited number of characters on which to differentiate taxa, though cuticular analysis of foliage appears to indicate large numbers of species (Šimůnek 2000, 2007; Šimůnek and Florjan 2013). High diversity is supported not only by the wide distribution of the plants but also by the enormous range of variability in their growth habits (fig. 10A, 10B), from scrambling forms (Rothwell and Warner 1984), to small trees (Cridland 1964), to large, woody trees of tall stature (Falcon-Lang and Scott 2000; Falcon-Lang and Bashforth 2004, 2005; Šimůnek et al. 2009; Césari and Hünicken 2013). The broad range of habitats encompassed by species of this lineage also suggests and is consistent with high species diversity (Šimůnek 2000, 2007, 2008); cordaitaleans were found throughout the Pennsylvanian tropical realm and were important in Cathyasian eastern Pangean floras during the Permian (Hilton et al.

2009). The group also extended into the high latitudes, particularly in the Permian, and so was of global distribution (Meyen 1987; Césari and Hünicken 2013).

Dryland Floral Composition

Pennsylvanian-age dry tropical floras can be difficult to characterize because they often are not well preserved or are transported and also because the landscapes they occupied were more environmentally heterogeneous than wetlands. Proportionately, a relatively small part of the Pennsylvanian floristic literature describes seasonally dry floras, often referred to as upland or extrabasinal (Havlena 1970; Pfefferkorn 1980; Dimitrova et al. 2011). The fossil remains of such floras are generally relatively monotonous in terms of dominance patterns, composed mainly of seed plants, though they appear to have been moderately diverse, based on well-preserved assemblages. Two qualitatively distinct kinds of seasonally dry assemblages occurred periodically in Pennsylvanian lowlands (DiMichele et al. 2010), with overlaps between them: cordaitalean dominated, particularly in the Early and Middle Pennsylvanian, and conifer dominated, particularly in the Late Pennsylvanian (fig. 11). There also may have been edaphic specialist floras,
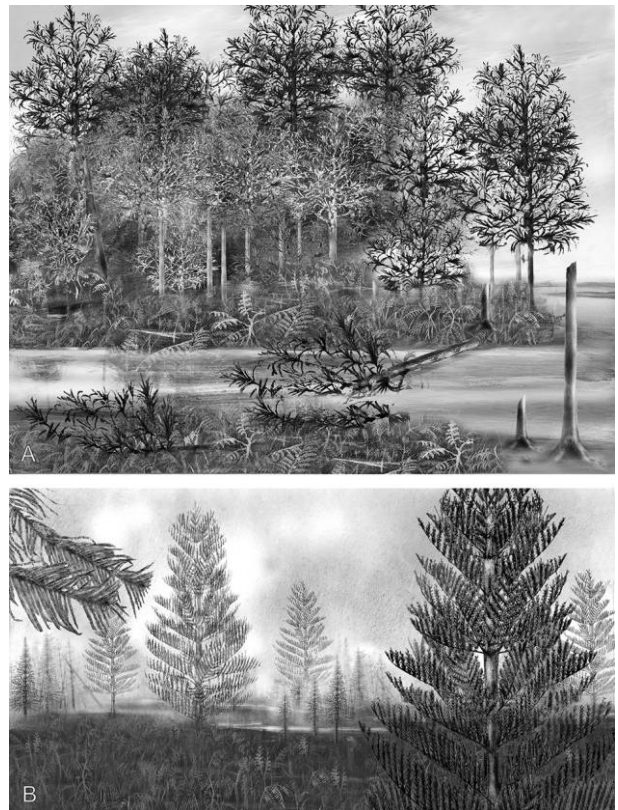

Fig. 11 Dryland landscapes. *A*, Cordaitalean forest dominated by large trees in dense stands. Seed ferns and ferns in the understory and as ground cover. *B*, Walchian conifer open woodland. Ground cover of small pteridosperms or ferns (although we know the foliage of these plants, we know very little about their growth architectures). Calamitaleans line a stream in the background. Reconstructions by Mary Parrish, Smithsonian Institution.

often found on thin soils with poor water-holding capacities, frequently developed on limestones. This is quite likely a considerable oversimplification, given the magnification of variability in soil moisture deficits across landscapes when rainfall is seasonal; it is challenging, however, to characterize such vegetation based on the limited fossil record.

Seasonally dry floras from coal basins of the central and west-central Pangean equatorial region are often represented by allochthonous elements (transported from outside the habitat of burial and preservation; Condon 1997; Gastaldo and Degges 2007; Gibling et al. 2010), though parautochthonous (transported but within the habitat of growth) and in situ assemblages are known (Cridland and Morris 1963; Winston 1983; Mapes and Rothwell 1988; McComas 1988; Falcon-Lang 2006; van Waveren et al. 2008; van Hoof et al. 2012; Bashforth et al. 2014). From the Late Mississippian to the Middle Pennsylvanian, such floras, where they are known, appear to have been dominated by cordaitaleans of large stature (fig. 10A; Falcon-Lang 2003b; Falcon-Lang and Bashforth 2005; Bashforth et al. 2014). Walchian conifers appeared during the Middle Pennsylvanian (fig. 10D), perhaps during a change to greater rainfall seasonality at all phases of glacial-interglacial cycles (Cecil 1990; Bashforth et al. 2014), and became an increasingly important element of these kinds of assemblages (Galtier et al. 1992; Rothwell et al. 1997; Hernandez-Castillo et al. 2001b; Blake et al. 2002; Falcon-Lang et al. 2009; Plotnick et al. 2009). Plants of both lineages are coniferophytes and had strongly xeromorphic morphological features (Clement-Westerhof 1988; Rothwell et al. 1997; Šimůnek 2000, 2007; Šimůnek et al. 2009). They are accompanied in the better-preserved assemblages by various elements not typically found in wetland floras. These accessory taxa differ to a large degree between the cordaitalean- and coniferalean-dominated assemblages. Those associated with the older cordaitalean-rich assemblages have strong affinities with Mississippian plants from seasonally dry settings (Wagner 2001; Bashforth et al. 2014). The Late Pennsylvanian conifer-enriched floras include such plants as callipterids and taeniopterids (Cridland and Morris 1963), which have affinities with lineages that became prominent in the Permian (DiMichele and Aronson 1992; Kerp 1996), although some of the Mississippian-type elements persist into the later Pennsylvanian and Permian as well (Mamay 1968, 1992; Šimůnek and Bek 2003; Tidwell and Ash 2003; Wang and Chaney 2010). Nearly every seasonally dry flora also includes a few stereotypically wetland taxa, particularly calamitaleans and tree ferns, both of which persist well into the Permian. These are sometimes accompanied by the aborescent lycopsid *Sigillaria*, a plant that may have had various kinds of morphological and reproductive features permitting tolerance of drier conditions than other arborescent lycopsids (Phillips and DiMichele 1992; Pfefferkorn and Wang 2009), and by pteridosperms in older, cordaitalean-rich assemblages possibly with somewhat longer wet periods than those dominated by or enriched in conifers.

Cordaitaleans from seasonally dry settings are known from a wide range of preservational conditions from parautochthonous (Winston 1983; Falcon-Lang et al. 2009) to allochthonous. The parautochthonous deposits often represent small, channel-form accumulations in cratonic flatland settings (Cun-

ningham et al. 1993; Feldman et al. 2005; Falcon-Lang et al. 2009), with evidence from associated paleosols and sedimentary features of seasonal moisture regimes. The allochthonous deposits often occur as large accumulations of trunks in channel deposits, not infrequently as logjams (Calder 1998; Falcon-Lang and Scott 2000; Stanesco et al. 2002; Falcon-Lang 2003b; Gibling et al. 2010). The allochthonous deposits are found most often in proximity to documented upland areas, from which the logs are presumed to have derived (Falcon-Lang and Scott 2000; Falcon-Lang and Bashforth 2005). This kind of preservation, in particular, gives the impression that most of the cordaitaleans in such settings were quite large trees (fig. 10A), ranging upward of 50 m in height (Falcon-Lang and Scott 2000; Falcon-Lang and Bashforth 2004). Rare reports of autochthonous cordaitalean stumps still in place within seasonally dry paleosols fringing channels (Bashforth et al. 2014) and in alluvial fans (Falcon-Lang 2006) confirm large-sized trees in these habitats. Based on wood anatomy, several different species of large, woody cordaitaleans occupied such settings (Falcon-Lang 2003a). Cordaitalean species of large stature may have been the ultimate K-selected plants of their era (Bashforth et al. 2011), due to their large, woody stems, which can be presumed to indicate long life spans and relatively slower growth than most of their wetland counterparts. Dryland settings, however, also seem to have hosted smaller cordaitaleans (fig. 10B) with sprawling growth forms (Falcon-Lang 2007). The frequent association of cordaitalean remains with abundant coniferophytic charcoal has led to suggestions that fires were regular and important parts of the landscapes they dominated (Falcon-Lang and Scott 2000; Scott et al. 2010). As noted above, cuticular studies suggest that peat-swamp cordaitaleans were taxonomically distinct from those of more seasonally dry settings (Šimůnek and Florjan 2013).

Conifers, like cordaitaleans, are consistently associated with depositional environments, including paleosols, indicative of seasonally dry settings and with an abundance of coniferophytic charcoal, suggesting habitats subject to frequent fires (McComas 1988; Rothwell et al. 1997; Ziegler et al. 2002; Uhl et al. 2004; Falcon-Lang et al. 2009; Scott et al. 2010; Looy 2013). Again, as with the Cordaitales, many of the earlier conifer occurrences are from deposits formed proximate to contemporaneous mountainous areas in Europe, the Appalachian region, and New Mexico (Lyons and Darrah 1989; Galtier et al. 1992; Rothwell et al. 1997; Martino and Blake 2001; Blake et al. 2002; Lerner et al. 2009; Lucas et al. 2013, pp. 56–57). Late Pennsylvanian conifers are more common components of floras from intermontane or limnic basins in central Europe (Kerp 1996) than they are from the broad, flat cratonic areas of the North American coal basins, particularly from the Midcontinent and Illinois Basin regions (Rothwell et al. 1997); the relative rarity of conifers in both the Appalachian Basin and near-mountainous areas of the Iberian Peninsula, both close to active tectonism and associated elevated areas, is noteworthy (Blake et al. 2002; Eble et al. 2009; Wagner and Álvarez-Vázquez 2010; Bashforth et al. 2010). Hernandez-Castillo et al. (2003) reconstructed Late Pennsylvanian conifers as diminutive, 2 m tall, plagiotropically branched trees (fig. 10D), much like a juvenile of the extant *Araucaria heterophylla*, an interpretation consistent with the small Middle Pennsylvanian

coniferopsid stems identified by Galtier et al. (1992). Other possible Late Pennsylvanian coniferopsids, from a coastal habitat in New Mexico (Falcon-Lang et al. 2011*b*), suggest much larger woody trees (figs. 10*C*, 12*F*, 12*G*). And, certainly, by the Permian, these plants had attained relatively large stature (Looy 2013). Throughout their Paleozoic history, from the earliest occurrences (Hernandez-Castillo et al. 2009) to their abundant occurrences in the Permian (Florin 1950; Kerp et al. 1990; Kerp 1996; Ziegler et al. 2002; DiMichele et al. 2007; Looy and Duijnstee 2013), conifers were probably the most consistently reliable indicators of environments with seasonal moisture stress; Ziegler et al (2002) mapped their paleogeo-

graphic distribution and found them to be restricted to seasonally dry environments of the Euramerican tropics and subtropics. The consistent association with indicators of periodic drought led White (1936) to call them "children of adversity."

There was an array of other plants associated with seasonally dry floras. Most are encountered much less commonly than conifers and cordaitaleans, depending in part on the ability of their foliage to survive transport, burial, and decay. Bashforth et al. (2014) refer to these as enigmatic elements and note changes in these elements in concert with changes in the dominant cordaitaleans and conifers. Enigmatic elements in Early and Middle Pennsylvanian cordaitalean-dominated flo-
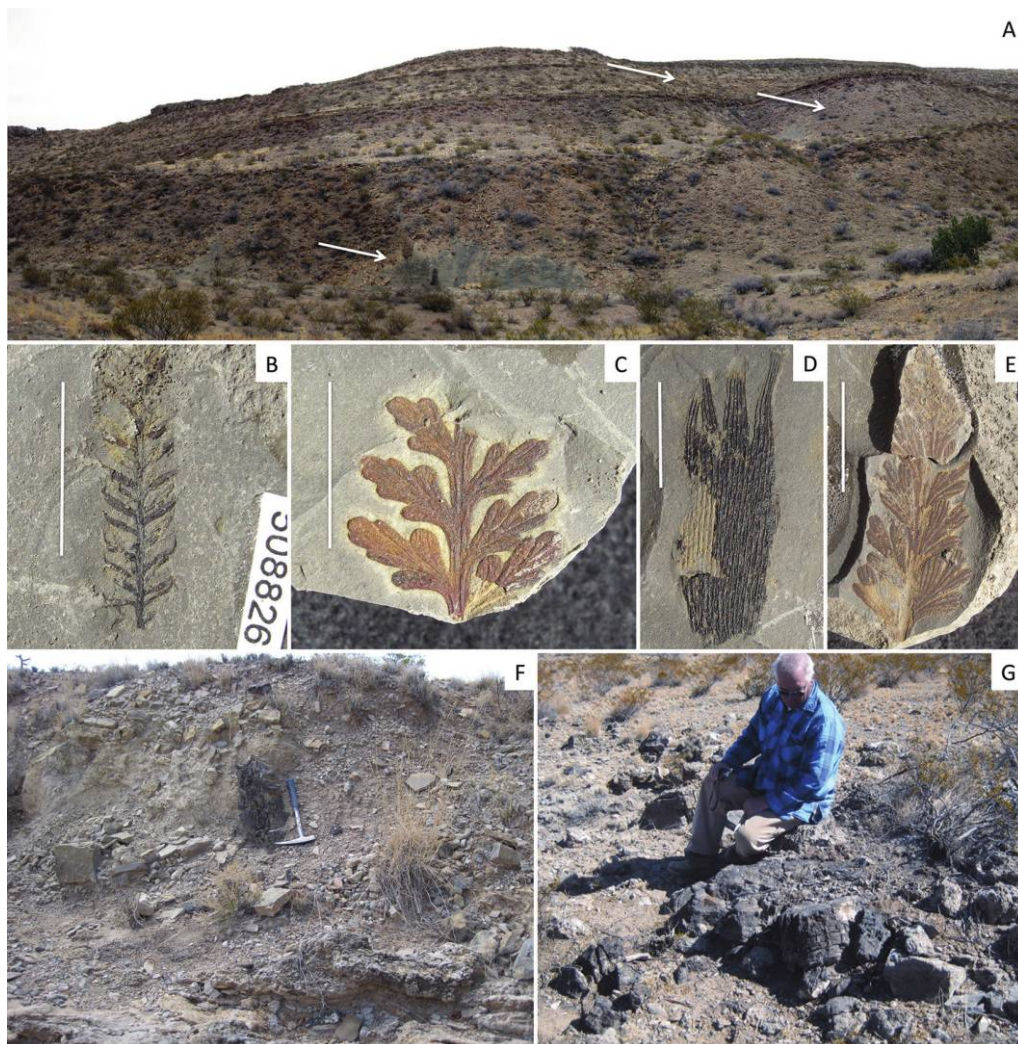

Fig. 12   Middle and Late Pennsylvanian (Desmoinesian and Missourian) seasonally dry floral elements and depositional environments. Cerros de Amado area, east of Socorro, New Mexico. *A*, Series of stacked, coarsening-upward deltaic lobes (arrows). Mudstones contain both transported plant remains and mixed brackish and marine invertebrate fauna. *B*, Walchian conifer. *C*, *Sphenopteridium* of the *Sphenopteris germanica* type, a pteridosperm with Mississippian affinities. *D*, *Charliea manzanitana*, a noeggerathialean with Early Pennsylvanian affinities. *E*, Callipterid, possibly *Lodevia* sp., a peltasperm. This specimen was collected from rocks of Early Missourian age. *F*, Coastal deposit of Late Pennsylvanian (Missourian) age, containing upright coniferalean tree trunks. Dune deposits consisting of carbonate and gypsum embed a small upright trunk (dark area next to digging tool). Trunk base is covered but is surround by tufa (the frothy material near the bottom) and is rooted in a micritic limestone, just visible below the tufa. *G*, Naturally exhumed tree base of large diameter. Roots are visible; these are embedded in a micritic limestone visible below scattered pieces of tufa, which surrounds the tree base above the limestone rooting horizon. Scale bars in *B*–*E* = 1 cm.

ras are most noteworthy for the strong Mississippian affinities of many of the taxa, including species of *Adiantites*, *Rhacopteridium*, and *Sphenopteridium* (Wagner 2001). Also included among these cordaitalean associates are the possible edaphic specialist plants *Megalopteris* and *Lesleya* (fig. 13*A*, 13*B*), which perhaps favored thin, droughty limestone soils, and possible noeggerathialeans (fig. 13*C*, 13*D*), an enigmatic group of uncertain affinity (Leary and Pfefferkorn 1977; Tidwell and Ash 2003). *Lesleya* has been suggested as a possible cycad precursor (Leary 1990) or an ancestor of the Gondwanan glossopterids (Leary 1993). Bashforth et al. (2014) and Wagner (2005) also report *Dicranophyllum*, a probable coniferophyte (Barthel and Noll 1999), species of which persist into the Permian. Accompanying the rise of conifers, probably reflective of increased seasonal drought during the drier phases of glacial-interglacial cycles (Bashforth et al. 2014), a new suite of seasonally dry subdominants appears, types more typically associated with Permian floras, many of which are strongly xeromorphic (figs. 12, 14). These include such plants as *Taeniopteris*, a polyphyletic form taxon among which are possible cycad precursors (Cridland and Morris 1960; Mamay 1976; Kerp 1983; Winston 1983; Gillespie and Pfefferkorn 1986;
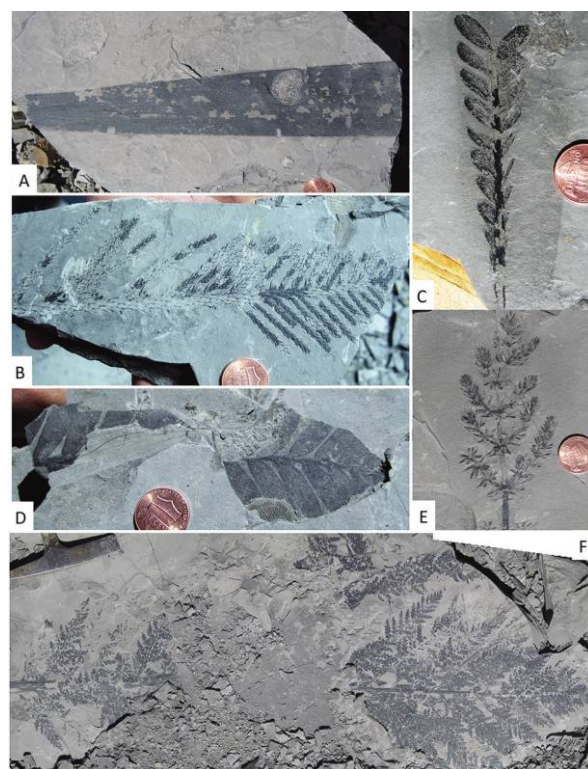

Fig. 14 Mixed seasonally dry flora from the Kinney Clay Pit, Late Pennsylvanian (latest Missourian) of New Mexico. All specimens were photographed in the field. *A*, *Cordaites* leaf. *B*, Walchian conifer branch. *C*, *Plagiozamites* leafy axis, possibly cycadophytic affinities. *D*, *Charliea manzanitana* foliage. *E*, *Annularia* sp., similar to *Phyllotheca paulinensis*. *F*, *Sphenopteridium manzanitanum*, nearly complete leaf. Penny is 19 mm in diameter.

Axsmith et al. 2003), as well as ferns (Remy and Remy 1975). Early members of the callipterid peltasperms, such as *Dichophyllum*, *Rhachiphyllum*, and *Lodevia* (Cridland and Morris 1963; Šimůnek and Martínek 2009; Pšenička et al. 2011); additional cycadophytic elements, such as *Plagiozamites* (Bassler 1916); and coniferophytes, such as *Podozamites* (Mamay and Mapes 1992), also have been reported. Noteworthy among those persisting from the earlier Pennsylvanian and later Mississippian are *Sphenopteridium*, *Dicranophyllum*, and the noeggerathialean *Charliea* (Mamay and Mapes 1992; Tidwell and Ash 2003; DiMichele et al. 2013*b*; figs. 12*C*, 12*D*, 13*D*, 14*D*, 14*F*, 15*C*, 15*D*).

Plants typically identified as having wetland affinities are a highly variable component of seasonally dry assemblages (fig. 16). The most consistently present are the calamitaleans, which have been identified in wet areas surrounding lakes and streamsides or in bars within streams (Falcon-Lang et al. 2004; Falcon-Lang et al. 2012; Bashforth et al. 2014). Tree ferns also are commonly found in similar settings, particularly in Middle and Late Pennsylvanian assemblages, reflective of their colonizing abilities and rapid growth capacities. The pteridospermous component often includes taxa not typical of or found in abundance in wetland vegetation intimately associated with coals.

Fig. 13 Lower Pennsylvanian seasonally dry plants (*A–C*, *E*). *A*, *Lesleya* sp., University of Illinois specimen. *B*, *Megalopteris* sp., University of Illinois specimen. *C*, *Charliea guntheri*, Manning Canyon Shale, Utah, a noeggerathialean. *D*, *Charliea readii*, from the Pennsylvanian-Permian boundary, Carrizo Arroyo, New Mexico; specimen shown for comparison. *E*, *Sphenopteridium* sp., University of Illinois specimen. Scale bars = 1 cm. *C* and *D* reprinted from Tidwell and Ash (2003), with permission of Elsevier.
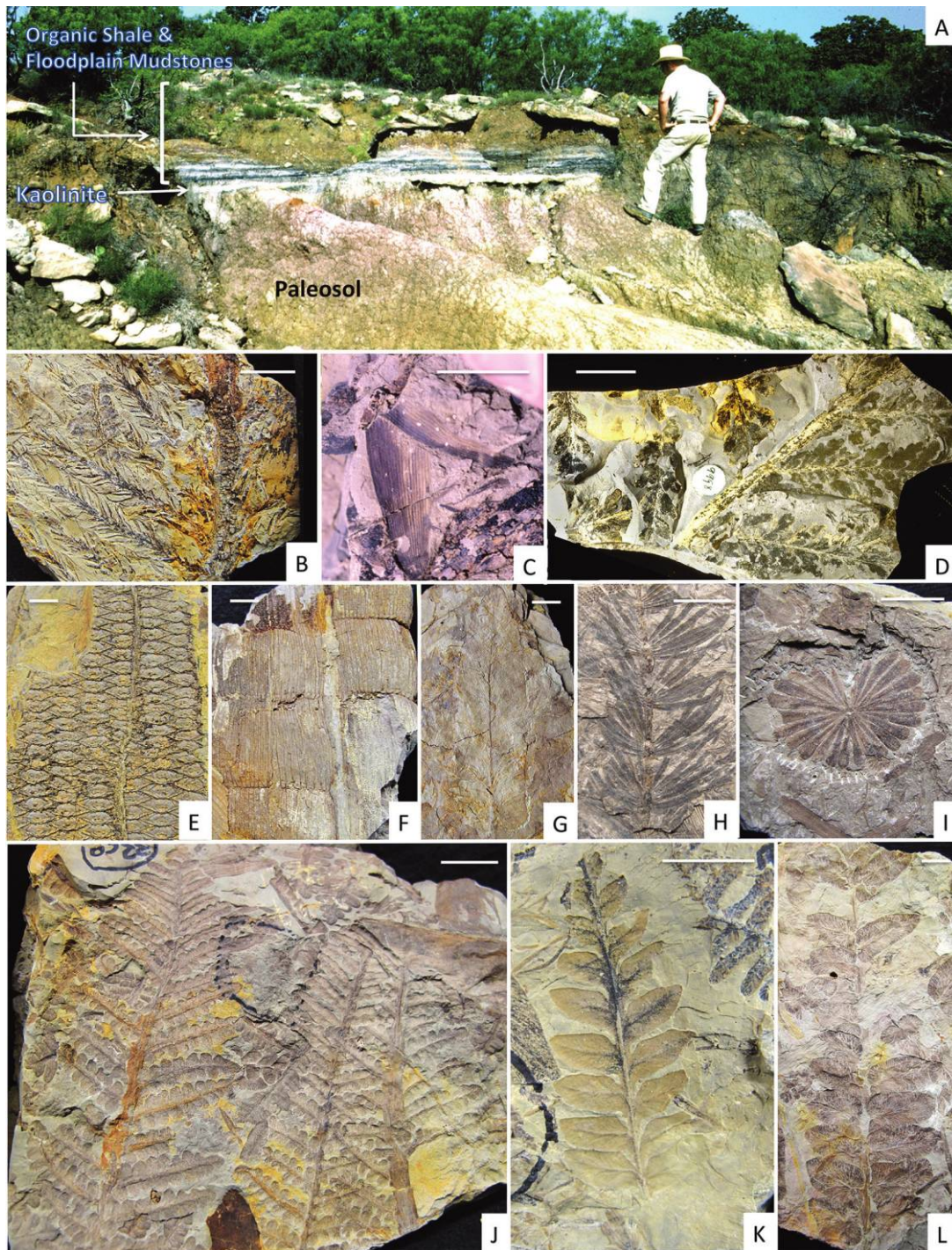
Fig. 15 Late Pennsylvanian (Virgilian) representative outcrop and fossils, from north-central Texas. This outcrop represents a typical cyclothem from this region of the Eastern Shelf of the Midland Basin, in which there are few marine strata. Seasonally dry flora and wetland flora are intercalated, in beds of different lithology. *A*, Characteristic lithological sequence: paleoultisol, indicative of wet but well-drained conditions; kaolinite bed in erosional contact with paleosol, possibly formed in a standing water lake. Organic shale, swamp deposit. Mudstones and siltstones formed in a wet floodplain setting. Blocks of sandstone at the top of the outcrop. *B–D*, Flora of the kaolinite bed. *B*, Walchian conifer. *C*, *Charliea* or *Yuania* noeggerathialean leaf. *D*, *Sphenopteridium* sp. of the *Sphenopteris germanica* type. *E–H*, Flora of the organic shale bed. *E*, *Sigillaria brardii*; lycopsid bark. *F*, *Calamites* stem; sphenopsid. *G*, *Macroneuropteris scheuchzeri*; pteridosperm and the dominant element of the organic shale beds. *H*, *Asterophyllites equisetiformis*; calamitalean foliage. *I–L*, Flora of the floodplain mudstones. *I*, *Annularia carinata*; calamitalean foliage. *J*, *Pecopteris puertollanensis*; tree fern foliage. *K*, *Pseudomariopteris cordato-ovata*; scrambling to climbing pteridosperm. *L*, *Neurodontopteris auriculata*; pteridosperm foliage. Scale bars = 1 cm.
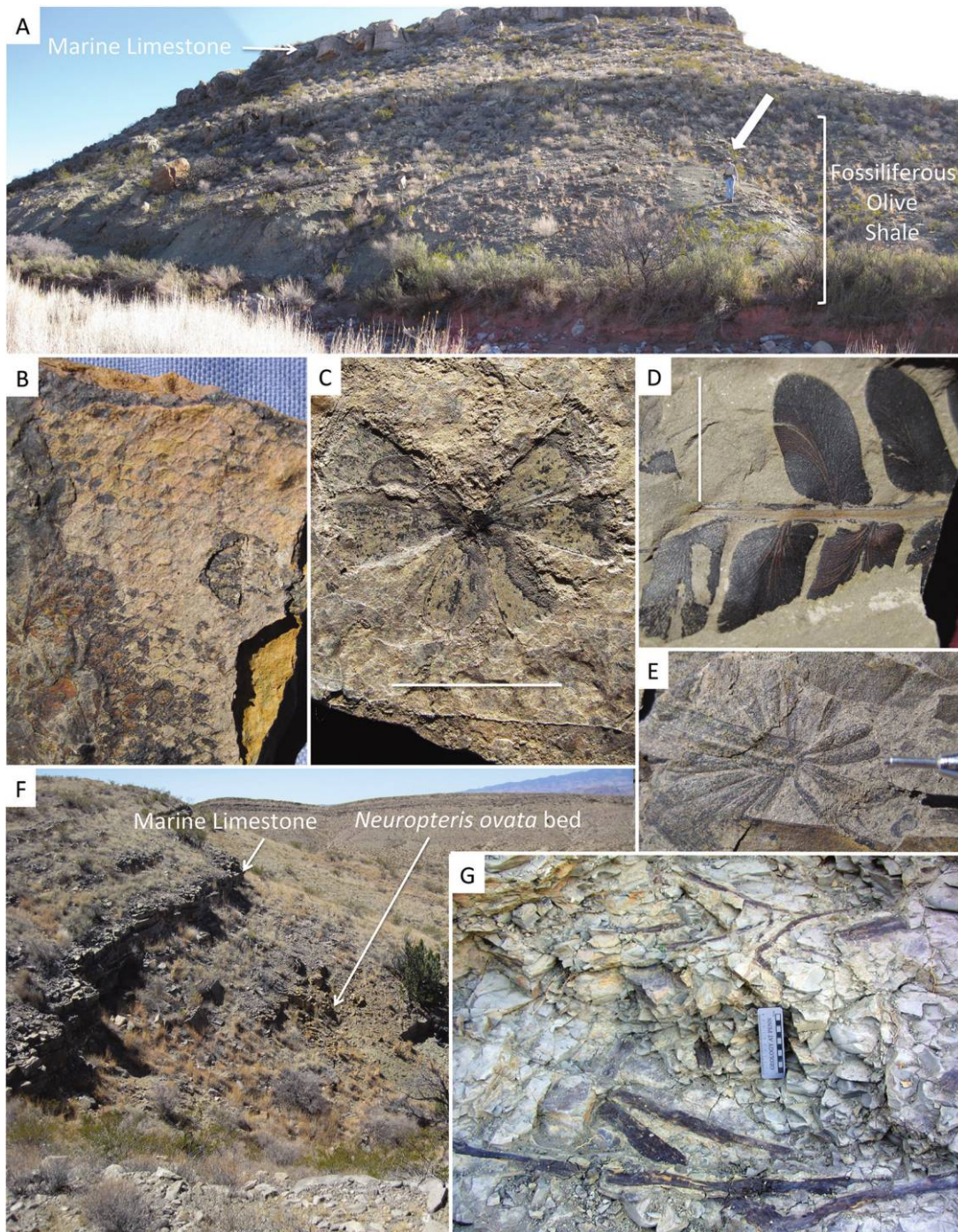
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Fig. 16 Middle and Late Pennsylvanian (Desmoinesian and Missourian) wetland floral elements and depositional environments. Cerros de Amado area, east of Socorro, New Mexico. *A*, Olive siltstone bearing a mixed seasonally dry and wetland allochthonous flora. *B*, *Sigillaria brardii*. *C*, *Sphenophyllum oblongifolium*; ground cover sphenopsid. *D*, *Neuropteris ovata*; pteridosperm foliage. *E*, *Annularia* sp.; calamitalean foliage. *F*, *Neuropteris ovata*; autochthonous accumulation in a clastic, coastal swamp habitat. This exposure crops out in an area of several hundred hectares. It is overlain by a marine limestone that marks the Middle–Late Pennsylvanian (Desmoinesian-Missourian) boundary. *G*, The deposit contains thickly interlayered stems, foliar axes, and laminate foliage consisting predominantly of *N. ovata*. Scale bars in *C* and *D* = 1 cm. Pencil tip in *E* = 1 mm. Ruler in *G* = 10 cm.

The lycopsid *Sigillaria* occurs in dryland habitats into the Early Permian Texas redbeds (DiMichele et al. 2006*b*, their fig. 14C).

The presence of wetland elements in floras dominated by seasonally dry vegetation should not be a surprise—wetter areas exist within many dry landscapes, even deserts, and species adapted for high soil moisture conditions are able to colonize parts of these landscapes, such as stream and lake margins, springs, and local swampy areas. What is unusual, however, is the taxonomic similarity, or even identity, of the species in wet patches of dry landscapes and the species of widespread, vast wetland landscapes. Dispersal constraints were much less limiting in wetlands than in drylands due to spatial habitat continuity in the former. In seasonally dry landscapes, these same taxa would have had to disperse between small, discontinuous patches of wetlands or remain confined to wetland riverine corridors. Perhaps the compositional similarity of wet substrate species, regardless of background climate, mainly reflects the significantly lower species diversity of that time, compared to what we take for granted today. With many fewer species, each may have had broader patterns of resource use (considering species to be shorthand for niche). Thus, with fewer species to do the job, one might hypothesize less competitive exclusion or exclusion by simple incumbency among those species specialized for any given set of physical conditions.

Biogeography-Spatial Dynamics of the Biomes

Climate models and geological evidence, as referred to above, suggest several trends that require examination of the spatial dynamics of the plants. First, it is clear that equatorial climate oscillated during glacial-interglacial cycles between wetter and drier phases, linked to fluctuations in sea level and likely driven by changes in ice volume (figs. 3, 4). Second, there is considerable evidence for an interval of strong global warming in the early part of the Late Pennsylvanian (roughly the Missourian/Kasimovian), probably associated with nearly complete melting of Southern Hemisphere ice (Fielding et al. 2008). And, finally, much physical evidence indicates a long-term trend of increasing equatorial aridity during the Pennsylvanian and into the Permian (Tabor and Poulsen 2008) on which glacial-interglacial fluctuations were superimposed; thus, through time and on average, the drier parts of cycles got more dry and the wetter parts less wet. In association with these climatic changes, there must have been changes in the areal extent of wetland and seasonally dry biomes across the Pangean tropical realm and certainly in the central and western Euramerican parts of the supercontinent, on which this review is focused. Perhaps this is most clearly revealed by instances where the wetland and seasonally dry vegetation types occur in different beds, representing distinct lithologies and depositional environments, within the same outcrops (fig. 15). Such occurrences indicate temporal and, thus, spatial separation of these biomes.

Fate of the Wetland Flora during Dry-Climate Intervals

In light of the many strong geological indicators of repeated climate changes in the equatorial Pangean tropics, the question of what happened to the coal swamps when it was not wet has rarely been asked. This is likely because the wetlands are so prominently represented in the Pennsylvanian tropical fossil record; this has led to the assumption that large swaths of megawetlands were always present, somewhere on the landscape. In contrast, hypotheses about the location and underlying causal factors of dryland floral composition and location, the so-called upland or extrabasinal associations, have been subjects of discussion in Carboniferous paleobotany since such floras were recognized—their rarity as elements of the fossil record has given them an exotic aura. The lack of investigation of the fate of wetlands during periods of dry climate reflects, perhaps, the long-held view that the equatorial lowlands of the Pennsylvanian were perpetually "wet"; it was, after all, the Coal Age, and coal means wet climate (Cridland and Morris 1963; Lyons and Darrah 1989; Broutin et al. 1990; Dimitrova et al. 2011). Consequently, in this view, the fate of wetlands through any particular glacial-interglacial cycle is a nonquestion; they were always there under an unchanging, humid background climate.

The ever-present-wetlands model generally points to the dynamics of fluvial, coastal, and deltaic sedimentation to create habitat heterogeneity (Horne et al. 1978; Ferm and Weisenfluh 1989) within which peat-forming wetlands, clastic swamps, and wet mineral soil habitats and even local well-drained settings were always somewhere present and in close proximity to one another. In such models, the siliciclastic and carbonate beds that separate coal seams reflect, through time, the local spatial variation found on the landscape. It is through such interpretations that the strata between coals can come to be attributed to short-term flood events, separating long-lived coal swamps (Dimitrova et al. 2011; but for a climate-based interpretation of the same location, see Dolby et al. 2011). Explicitly or implicitly, this model of the Pennsylvanian lowland assumes constant background climate, one that was favorable for peat formation to be ever present on the landscape, somewhere. Confounding data that such models generally do not address include paleosols indicative of long periods of seasonal drought (figs. 4, 5) located between many coal beds (Tandon and Gibling 1994, 1997; Driese and Ober 2005; Rosenau et al. 2013*a*, 2013*b*) or changes in sedimentological patterns linked mechanistically to background climate regimes (Calder 1994; Batson and Gibling 2002; Cecil and Dulong 2003; Theiling et al. 2012; Opluštil et al. 2013*a*).

Another way to look at this problem is to propose that peat/coal formation is not a function of wet climates but only a result of the ponding of groundwater. In the broad, flat, cratonic settings such as the interior areas of west-central Pangea (Watney et al. 1989), such ponding is most often envisioned to be caused only by rising sea levels linked to glacial-interglacial cycles (Bohacs and Suter 1997), thus creating bands of coastal swamps that move inland ahead of the sea. As discussed above, these models do not account for the great contrasts in the rates of peat accumulation and the rates of sea level rise in response to pulse-like ice melting (Archer et al. 2014), or for why coals are not present in areas of demonstrably drier climates, such as western equatorial Pangea, which also experienced glacially driven sea level rises and falls (Bishop et al. 2010; Elrick and Scott 2010), or for the extensive evidence that the vast Pennsylvanian coal swamps did not form as narrow bands proceeding landward as sea level rose but appear, instead, to be blanket deposits, time-equivalent throughout (Greb et al. 1999*b*, 2003; Cecil et al. 2003), thus requiring a

mechanism that would generate widespread wet conditions (i.e., climate). They also must explain why peat deposits of Pennsylvanian coal quality do not fringe the margins of every landmass on our modern Earth, given that sea levels have been rising since the last glacial maximum. Less common, but also suggested, is that wetlands formed by the ponding of groundwater draining from uplands into the low ground. Calder (1994) presents a compelling case for this, one still strongly linked to climate cyclicity and its effects on sedimentation, although with major consideration given to the effects of local tectonism in a highly active area. There are suggestions, however, that this kind of moisture source also can promote peat formation under uniformly seasonally dry climates (Chandler 1998). Were this possible, coals should be a common component of strongly seasonal Pennsylvanian landscapes of the mountainous portions of western Pangea (Cecil et al. 2003b; Peyser and Poulsen 2008; Tabor and Poulsen 2008; Tabor et al. 2008; Nelson et al. 2013b) and even of seasonal-climate Permian red-bed landscapes proximate to upland areas (e.g., Rotliegends [Kerp and Fichter 1985; Howell and Mountney 1997; Rieke et al. 2003], Lodève [Schneider et al. 2006; Galtier and Broutin 2008], north-central Texas [Chaney and DiMichele 2007; Nelson et al. 2013a]), which they are not. Thus, humid climates appear, even in tectonically active areas, to be required for peat formation in the tropics.

It is not the intention here to imply that wetlands, sensu lato, invariably reflect humid climates. Any consideration of the ecosystems in our modern world shows such a generality to be unsupportable. What is explicitly intended, however, is the recognition that vast wetlands of Pennsylvanian spatial scales and, particularly, peat-forming wetlands both today and in the past are indeed reflective of widespread humid to perhumid climates in almost all instances. Peat, in this case, is restricted to low-ash organic accumulations that might become coals following burial and diagenesis. This assertion is underpinned by the high degree of sensitivity of plants to both local habitat conditions and overall climatic conditions. Although local conditions are the final arbiter of what grows at any spot on the ground, these must be assessed within the context of the larger-scale regional climate.

Furthermore, consideration should be given to the way any local community of organisms is assembled; plants must be able to (1) get there, (2) survive there, and (3) compete there (Belyea and Lancaster 1999; Weiher et al. 2011). When considered in this light, dispersal limitation may be the strongest filter in this process and may have constrained the distribution of Pennsylvanian plant populations on many spatial scales (Laveine 1997; Hilton and Cleal 2007). Such local community-assembly controls are superimposed on glacial-interglacial fluctuations and the large and growing body of evidence that these were accompanied by and coordinated with widespread climatic changes.

Wetland-plant distributional patterns during glacial-interglacial cycles. Within the context of fluctuating climates, tied to the dozens of Pennsylvanian glacial-interglacial cycles, there are two competing hypotheses for the fate of wetland vegetation during the long, seasonally dry portions of these cycles (Falcon-Lang and DiMichele 2010). (1) The coal swamps and surrounding mineral substrate wetlands with high soil moisture requirements moved their location as climate changed during a glacial-interglacial cycle, tracking wet climates out of the tropical latitudes or into tropical or paratropical areas where wet climates persisted. (2) The dominant coal swamp and other wetland species retreated into refugia on the seasonally dry landscapes, occupying only much-reduced and likely spatially discontinuous small inland swampy areas, streamside and lakeside habitats, and coastal wetlands. A third possibility allows for these two biogeographic phenomena to occur simultaneously in latitudinally distinct parts of the tropical regions. Due to uncertainties in models and conflicts in their applications to geological strata in different paleogeographic areas, we cannot differentiate among these with certainty, though hypothesis 2 seems to be the more likely.

Hypothesis 1. In the equatorial regions of west-central and western Pangea, there are both empirical evidence and experimental climate model results for the episodic appearance of widespread wetlands separated by time intervals during which conditions suitable for extensive, regionally widespread wetland development were limited or absent. Thus, there does not appear to have been regional-scale spatiotemporal continuity of extensive wetland environments through all phases of a glacial-interglacial cycle (Cecil et al. 2003b; Eros et al. 2012; Rosenau et al. 2013a, 2013b). Thin coals, locally of minable thickness, appear to occur during some interglacials, often forming in deltaic settings during late highstand and sea level fall, but these are separated from lowstand coals by strata that record conditions physically and climatically unsuitable for peat formation. Recent models of Pennsylvanian climate (Poulsen et al. 2007; Peyser and Poulsen 2008; Horton et al. 2012) find little evidence of vast wetlands in tropical or paratropical regions during the drier phases of glacial cycles, which in such models are the interglacials. The modeling experiments of Horton et al. (2012), focused on changes in climate at the temporal scale of a glacial-interglacial cycle (cyclothem scale), suggest, or at least leave open, as discussed above, the possibility that areas of very high though seasonally distributed rainfall occurred during early interglacials in the Pangean equatorial regions. These data and experimental models do not lend support to the possibility of the continuous existence of vast areas of wetlands within the tropics or in paratropical areas during interglacials.

Hypothesis 2. In contrast to the mass-migration scenario, there is scattered but reasonably good evidence for the survival of wetland taxa within west-central and central Pangean equatorial basins, in wet streamside settings, channel belts, and localized wet areas within otherwise seasonally dry landscapes. For example, Elrick et al. (2013) report tidal mudflat floras during early interglacial stages, associated with the onset of continental flooding. The dominant plants in these weakly seasonal wetlands are pteridosperms, tree ferns, and the lycopsid tree *Sigillaria*, suggested to presage major compositional changes that occurred in wetlands at the Middle–Late Pennsylvanian boundary in response to what appears to have been a period of anomalously dry climate (Phillips et al. 1974; Falcon-Lang et al. 2011a). Similar floras were found preserved in small channels between both Middle and Late Pennsylvanian coal beds in the Illinois Basin. One, an intermittent discharge channel, was located between two major late Middle Pennsylvanian coals, collected by W. DiMichele and colleagues (fig. 17). This channel was found to contain several horizons of in
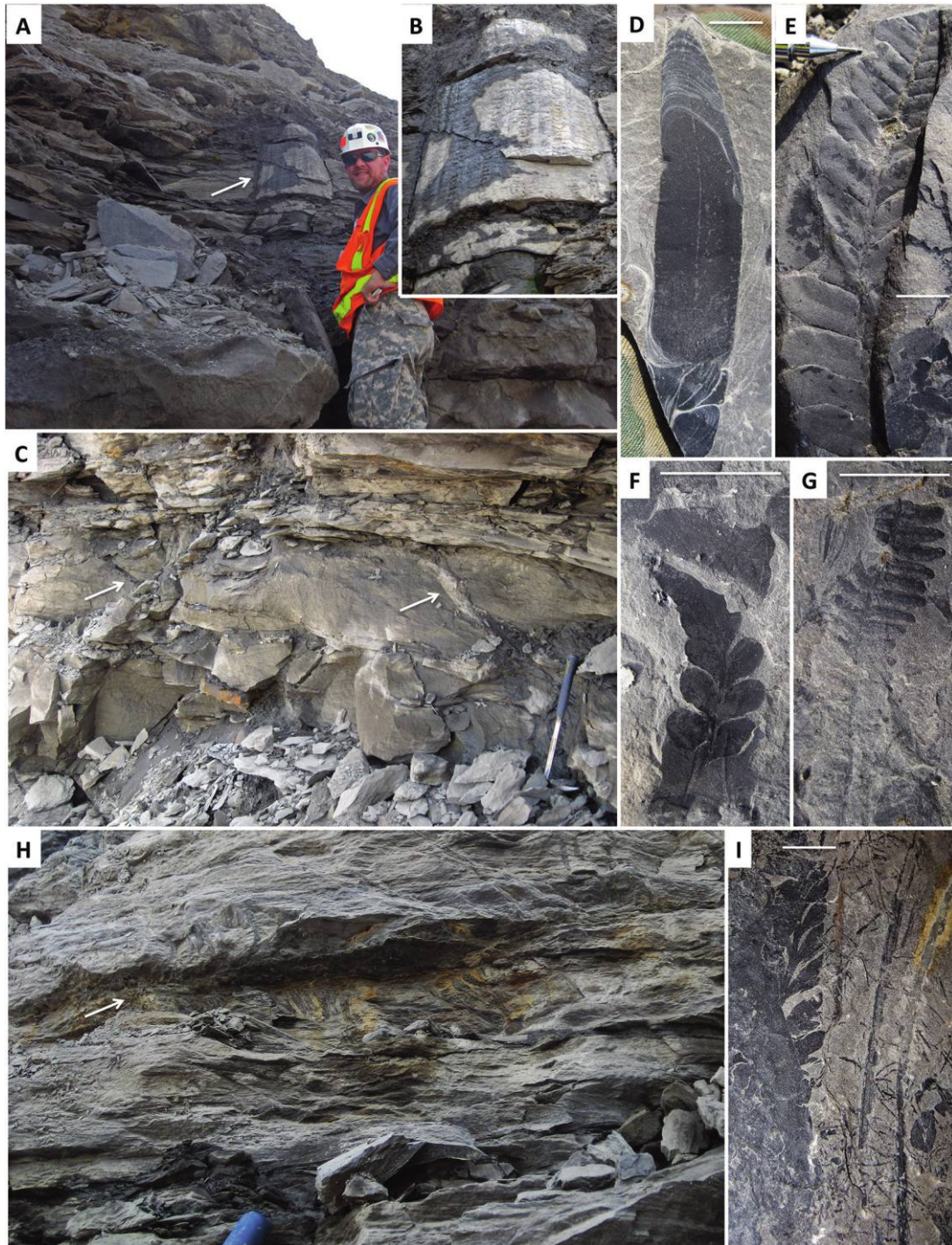
Fig. 17 Small, flashy discharge channel between the Baker and Danville coals, Middle Pennsylvanian (Desmoinesian) of Indiana. There are multiple horizons of rooted plants within the channel. *A, Sigillaria* tree base in upright position (at arrow), rooted within channel. *B,* Enlargement of *Sigillaria. C,* Pteridosperm stems rooted in the channel (arrows), deformed by burial in flood-borne sediments. *D, Macroneuropteris scheuchzeri*; pteridosperm foliage. *E, Neuropteris ovata*; pteridosperm foliage. *F,* Cf. *Odontopteris* sp.; pteridosperm foliage. *G, Pecopteris* cf. *vestita*; tree fern foliage. *H,* Stigmarian root system of lycopsid tree (arrow), within channel sediments. *I,* Pteridosperm roots and what is probably *Macroneuropteris scheuchzeri* pinnule in atypical preservation. Scale bars = 1 cm. Note pick handle base at bottom of *H.*

situ rooted plants, including the typical wetland elements *Macroneuropteris scheuchzeri*, *Neuropteris ovata*, *Lobatopteris* cf. *vestita*, calamitalean stems, and *Sigillaria*. The other channel was a small Late Pennsylvanian (Missourian) estuarine deposit that included *Cordaites* foliage as the dominant element, along with *Macroneuropteris* and calamitalean stem remains, and included strongly terrestrialized vertebrate remains, signifying general seasonal dryness of the landscape at the time of plant growth (Carpenter et al. 2011). None of the typically peat-swamp-centered lycopsid species was found, however, which is the most common—and puzzling—pattern. *Sigillaria* is by far the most commonly encountered lycopsid in such nonpeat, seasonal-climate wetland assemblages and is the dominant lycopsid in Euramerican wetland landscapes during the Late Pennsylvanian, suggesting that these channel deposits may have formed under more seasonally dry conditions than those that prevailed during formation of the widespread peat swamps/coals between which they occur. The Atlantic Canadian coal basins have proven particularly fruitful ground for the preservation of wetland elements in otherwise seasonally dry cordaitalean-dominated habitats from the Early Pennsylvanian (Falcon-Lang et al. 2006; Bashforth et al. 2014). Reports of wetland plants surrounding water holes suggest small, scattered refugia and, again, the only reported lycopsid being *Sigillaria* rather than elements of the typical peat-forming taxa (Falcon-Lang et al. 2004). Likewise, *Sigillaria* and calamitaleans are reported from within channels and streamsides as well as from cordaitalean-dominated vegetation (Falcon-Lang et al. 2006). Falcon-Lang et al. (2009) report a macroflora from a subcoal channel, formed laterally to a calcic vertisol (seasonally dry climate), dominated by cordaitaleans and including conifers, a seemingly typical example of an interglacial or early glacial seasonally dry flora (fig. 18*A*); the palynoflora derived from those same rocks, however, was dominated by *Lycospora granulata*, the spore of the arborescent lycopsid *Lepidopholoios hallii*, one of the most specialized wetland components of peat-forming swamps, suggesting the presence of these plants somewhere on that landscape. Similarly, Hawkins et al. (2013) were able to track vegetational changes through a single cyclothem in the Pennine Basin of the United Kingdom, and though they found distinct changes, including significant increases in dryland taxa, they also found a persistent signal of wetland plants through the entire profile.

Wetland plants in western Pangea. Wetlands, sometimes of considerable areal extent and consisting of basically the same flora as that typically found in siliciclastic rocks above coal beds—mudstone roof shales—in the central Pangean coal basins, existed throughout the western parts of Pangea during the Pennsylvanian. In this region of Pangea, peat swamps were of very limited development and then only during the Early and early Middle Pennsylvanian (Morrowan and Atokan; Gordon 1907; Kosanke and Meyers 1986). The floras from this time, Morrowan and Atokan, encompassed a considerable diversity of wetland species, including *Lepidodendron*, pteridosperms such as *Neuropteris*, and various calamitaleans (Tidwell 1967; Tidwell et al. 1992; Lucas et al. 2009). During the later Middle Pennsylvanian (Desmoinesian) and Late Pennsylvanian (Tidwell 1988; Tidwell et al. 1999; DiMichele et al. 2004, 2010, 2013*b*; DiMichele and Chaney 2005; Lerner et al. 2009; Lucas et al. 2013; Tabor et al. 2013*a*, 2013*b*), western

Fig. 18 Late Middle Pennsylvanian conifers from the Illinois Basin. *A*, Small channel below the Baker coal, laterally equivalent to the calcic paleovertisol below the coal. Channel base, marked by arrow, truncates underlying sediments. *B*, Conifer found in sediments derived from the channel (see Falcon-Lang et al. 2009). *C*, Cave from northern part of the Illinois Basin, filled with Pennsylvanian sediments. *D*, Conifer from the cave fill. *C* and *D* from Scott et al. (2010) used with permission of Elsevier.

wetland floras were less widespread and, as in the eastern coal basins, were greatly enriched in tree ferns, with a continued presence of pteridosperms and *Sigillaria* as the only tree lycopsid (figs. 15*E*–15*L*, 16*B*–16*E*).

Throughout the entire time interval, however, if examined on average, there are numerous western Pangean floras rich in wetland plants that also contain a significant number of taxa characteristic of seasonally dry environments. This is made most clear by transported assemblages, which are almost invariably mixed (fig. 14) and may be either dominantly dryland or wetland taxa, with a background of species from the other kind of vegetation (Lerner et al. 2009; DiMichele et al. 2013*b*). The implications of this are that, at times, these two floras were growing in close proximity, with the seasonally dry flora dominating the great majority of the land surface and the wetland flora fringing coastal areas and waterways. The almost constant presence of seasonally dry species in allochthonous assemblages indicates that the overall climate was seasonally dry. There also are examples of assemblages composed entirely of wetland species, the more typical and diverse of which are from older Pennsylvanian strata; these are, in almost all instances, parautochthonous to autochthonous and

thus not likely to reveal more than very local vegetation. Most such floras have not been published (we have a number of examples in the National Museum collections), but published examples include floras rich in lepidodendrids and other wetland species from the Mississippian-Pennsylvanian boundary in Arizona (Tidwell et al. 1992) and from strata of Atokan age in New Mexico (Lucas et al. 2009) and Colorado (Jennings 1980; for a humid-climate interpretation of this deposit, see Mack and Suttner 1977; Maples and Suttner 1990) and a late Desmoinesian-age autochthonous pteridosperm-dominated (*Neuropteris ovata*) coastal swamp deposit from New Mexico (fig. 16*F*, 16*G*), mentioned above, identified over several square kilometers (Lucas et al. 2013).

Glacial-interglacial cycles can be detected in parts of western Pangea during the Permian (Elrick and Scott 2010), though their expression can be strongly affected by local tectonism (Lucas and Krainer 2013). These cycles were accompanied by moisture fluctuations and associated variations in sediment transport patterns (Rueger 1996; Soreghan et al. 2002; Theiling et al. 2012), similar in kind, if not in detail, to those in the central Pangean coal basins. Such fluctuations should be expected to have affected the extent and location of wet and dry floras on the landscape, even in these consistently seasonal parts of western Pangea. It seems that during the drier intervals, the two floras lived in close enough proximity to produce mixed, transported floras in nearshore marine and lagoonal settings (Lucas et al. 2013). But during the wetter periods, the coastal areas covered by wetland vegetation enlarged and included small coastal swamps, and when preserved as parautochthonous deposits, the seasonally dry flora is rarely detected within these deposits as macrofossils (palynological investigations are very limited; Rueger 1996; Tabor et al. 2013*b*). This pattern continues into the Permian in this same region (White 1912; DiMichele et al. 2006*b*). In these younger rocks, wetland elements, represented mainly by tree ferns, occur sporadically, often in great abundance as dominants in parautochthonous deposits. In many other instances, tree ferns occur as allochthonous fragments. In either instance, the presence of wetland elements reflects their persistence in these seasonally dry Permian landscapes, likely in patches and along stream corridors.

Fate of the Dryland Flora during Wet-Climate Intervals

The presence of nonwetland elements in the Pennsylvanian tropics has been recognized for a long time (Gothan and Gimm 1930). Chaloner (1958) suggested the term "upland flora" to explain the presence of nonwetland plants in basinal areas. Because this term implicates areas of steep slopes, even if not mountainous areas themselves, and because plants, particularly in the Paleozoic, are likely to be found only in what were net sediment accumulating areas—basins—this term carries certain connotations about the habitats of nonwetland areas that may not be universally true. Pfefferkorn (1980) attempted to clarify this terminological problem by introducing the term "extrabasinal," thus implying only that the exotic species came from areas outside of basins, with no judgments regarding elevation.

Such basinal occurrences of nonwetland elements have been understood in various ways, but two explanations prevail. (1)

The explanation most often called upon is transport into basins from somewhere outside—that somewhere presumably drier and that dryness generally attributed to drainage due to elevation. (2) The other explanation calls for dispersal of the dryland floras into basins—again from outside—but in this instance from areas of seasonally dry climate, with the plants moving into the basins as climate there changed to seasonally dry.

Uplands and soil drainage.   The upland interpretation was (and remains?) by far the most prominent explanation for the sporadic appearance of dryland taxa in the lowland basinal fossil record. This is not as simple and straight forward a model as it may, at first glance, appear to be. In the most common formulation of this scenario, nonwetland plants are interpreted to have been transported into the lowlands from dry-soil habitats in surrounding upland areas. The dry soils in such settings are proposed to have been created solely by drainage on hills and slopes, not by climatic factors related to regional rainfall patterns. Thus, the populations of seasonally dry plants are proposed to have occupied well-drained areas at the same times that wetland plants occupied non-well-drained bottomlands. A generally unspoken corollary to this is that climate was constantly wet in the Pennsylvanian tropical belt, necessary to permit peat formation somewhere in the basinal bottomlands at all times (Remy 1975; Broutin et al. 1990; Dimitrova et al. 2010). These models generally do not explicitly call for changes in climate with increasing elevation, though this might be expected in mountainous areas if the mountains are high enough and could account for background pollen rain from conifers into lower-elevation intermontane wetlands (Broutin et al. 1990; Dimitrova et al. 2005, 2011; Falcon-Lang 2006; Bashforth et al. 2011; Dolby et al. 2011; Opluštil et al. 2013*b*).

In the most extreme version, the uplands are envisioned as small well-drained hills located within the lowland landscapes (Cridland and Morris 1963). In this scenario, dryland vegetation is closely surrounded by wetland flora, leaving drought-tolerant and obligate-wetland plants growing only meters apart in space (fig. 19, *top*). As noted by Zeigler et al. (2002), this is not the general idea that most people hold of uplands. Nor is this scenario likely under a humid or perhumid climate, where high rainfall would greatly mask or subdue the effects of drainage on small lowland hills.

In most models, uplands and basinal lowlands are envisioned as close together in space but separated by dozens to thousands of meters of elevation, with the elevated areas on the margins of the basins (fig. 19, *bottom*), such proximity facilitating transport of upland plant remains into basins (Havlena 1961, 1971; Lyons and Darrah 1989; Broutin et al. 1990; Cazzulo-Klepzig et al. 2007; Dimitrova and Cleal 2007). In another scenario, the upland plants become more recognizable during sea level highstands, when the depositional environments were pushed inland (Chaloner 1958; Neves 1958; Turner et al. 1994 [all palynoflora analyses]), effectively bringing the point of burial and preservation to the uplands with no need to account for climate change in association with mean sea level rise.

When long-distance transport of the plant material can be strongly supported empirically (such as in the cases of logjams within streams or charcoal fragments of a different kind from the flora in which they are embedded), the uplands are envi-
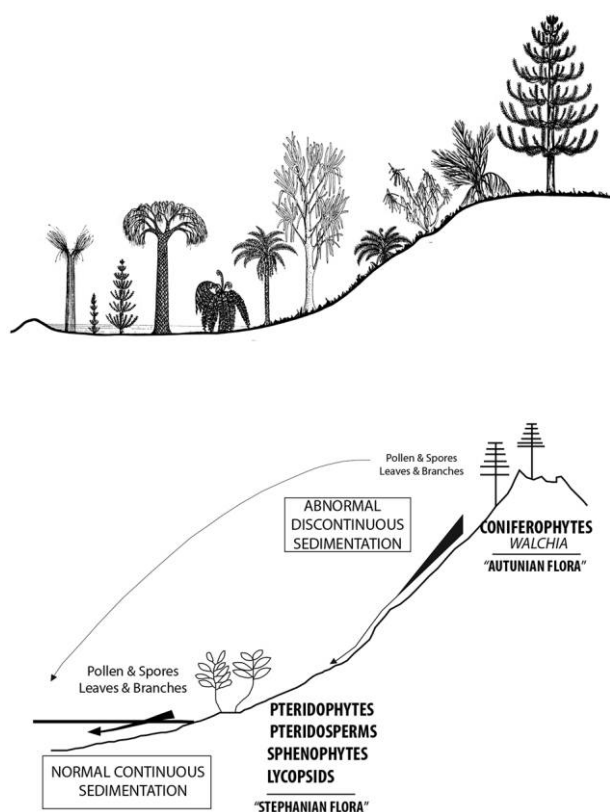
Fig. 19 The upland concept. Upper drawing is a figure taken from Cridland and Morris (1963; copyright © 1963, University of Kansas, Museum of Natural History, used with permission). It shows the upland flora and lowland wetland flora in close spatial proximity. The upland flora is envisioned as growing on local elevated areas within the basinal lowland, drainage-creating conditions that differentiate the two species pools. Lower drawing is modified from Broutin et al. (1990). In this model, the upland flora lives under essentially the same climate as the basinal wetland flora. Upland elements enter the basins mainly during periodic storm events that, through happenstance, coincide with parts of the plant life histories when pollen and seeds or branches are being shed (hence the label "abnormal sedimentation"). Upland plant remains may rarely enter the lowlands by being carried in streams. Different soil conditions, caused solely by drainage, separate the upland and lowland plants spatially. This diagram further implies that seeming stratigraphic differences (the Stephanian vs. Autunian floras) actually reflect different habitat preferences.

sioned as distant (Florin 1963; Falcon-Lang and Scott 2000; Uhl et al. 2004; Gastaldo and Degges 2007; Gibling et al. 2010). Under such circumstances, the role of climate is reduced in importance since transport might be expected to happen under any climate in which there was enough water movement to transport logs and/or plant debris long distances.

Climate control. In the other major view, nonwetland plants lived in areas of seasonal climate, whether uplands or extrabasinal lowlands; elevation is irrelevant to this model. The seasonally dry plants then invaded basins, cratonic or intermontane, during times of climate change in those basinal locations (Elias in Moore et al. 1936; Arnold 1941; DiMichele and Aronson 1992; Calder 1994; Gastaldo 1996; Blake et al.

2002; Ziegler et al. 2002; Šimůnek and Martínek 2009; Opluštil et al. 2013b; Tabor et al. 2013b). This view differs from the strictly upland view in that it explicitly includes a climatic element in the equation and recognizes that the natural landscape is climatically complex, biome distributions being mainly reflective of climatic patterns, primarily the interaction of climate and rainfall (Köppen 1936; Walter 1985). In addition, it places the dryland plants in the basins, not strictly on basinal fringes. Elevation, in such a scenario, may cause changes in the species composition within either the wetland or the seasonally dry biome (Šimůnek and Cleal 2011) but will account for whole-biome spatial differentiation only if it contributes to climatic differences (which is what the plants are actually responding to).

The climate control scenario is supported most strongly by occurrences of conifers, which are the most reliable, abundantly occurring indicators of seasonally dry conditions. Examples of conifers in places (a) far from any contemporaneous upland areas and (b) in beds mixed within coal-bearing stratigraphic sequences are illustrated for Middle Pennsylvanian occurrences in figure 18 and for Late Pennsylvanian strata in figure 15. Such conifer occurrences include the reports of Elias (in Moore 1936; see also Cridland and Morris 1963; Winston 1983; Feldman et al. 2005), Mapes and Rothwell (1988; see also Cunningham et al. 1993; Hernandez-Castillo et al. 2009), McComas (1988; see also Hernandez-Castillo et al. 2001b), Falcon-Lang et al. (2009; fig. 18A, 18B), Plotnick et al. (2009; fig. 18C, 18D), and Tabor et al. (2013b; fig. 15B). All are preserved under peculiar circumstances, between coal beds, but not as roof shales, representing falling stages of sea level and early lowstand portions of glacial-interglacial cycles, and in well-documented association with indicators of seasonal drought. It is in these parts of the cycles where climate models also, and independently, indicate that such seasonality is to be expected (Horton et al. 2012). These unusually preserved deposits serve as a reminder that seasonally dry conditions are most often highly unfavorable for the preservation of organic matter (Gastaldo and Demko 2011); while we might not usually look in such strata for plant fossils, it is, nonetheless, here that unusual floras are likely to be preserved.

Also indicative of climate are floras from intermontane basins of central Pangea, where conifers occur in parautochthonous assemblages, sometimes in association with callipterid peltasperms, including in close proximity to coal beds. Such occurrences strongly suggest resident populations in the local upland areas that moved into the intermontane basins during periods of regional climatic change (Šimůnek and Martínek 2009; Opluštil et al. 2013b). These macrofossil occurrences have been well constrained by sedimentary analyses, and it is clear that the plant remains were not subjected to long-distance transport from the uplands but rather were derived from populations living in the basins at the time of preservation. Such occurrences are an important indicator of habitat heterogeneity, which could have been considerable in these mountainous regions. A heterogeneity model, in combination with consideration of the response of plants to regional climate changes within these mountainous areas, could have important evolutionary implications, as documented for modern mountaintop islands (Hughes and Eastwood 2006; Kramer et al. 2011). In mountainous terrain, it is possible that extensive micro-

habitat heterogeneity was present through all parts of glacial-interglacial cycles due to variation in slope, aspect, and elevation and that dryland floras oscillated in coverage area as general climate changed. Such habitat heterogeneity is much less likely to have been found in the extensive flat cratonic areas of the American midcontinent (Watney et al. 1989), west of the Appalachians.

Biogeographic patterns. The seasonal climate model is tied more closely to the biogeography of seasonally dry floras than is the elevation drainage model, and it (the climate model) subsumes much of the matter of elevation, treating it as a significant modifier of local to regional climatic patterns. Based strictly on empirical data, referred to and discussed above, there appear to be three areas of the Euramerican tropical and paratropical belts in which plants adapted to seasonal drought may have resided permanently, during all phases of glacial-interglacial climatic fluctuations (fig. 20). In the Early and early Middle Pennsylvanian, such areas, dominated by cordaitaleans, are documented mainly in Atlantic Canada in central Pangea (Falcon-Lang and Scott 2000; Falcon-Lang 2003*b*, 2006; Falcon-Lang and Bashforth 2004; Dimitrova et al. 2011; Bashforth et al. 2014). In the late Middle and Late Pennsylvanian, conifer-rich to conifer-dominated floras appear to have resided in western regions of Pangea (Rueger 1996; Rothwell et al. 1997; Falcon-Lang et al. 2011*b*; DiMichele et al. 2013*b*) and in mountainous regions from the Appalachians through Atlantic Canada (Lyons and Darrah 1989; Falcon-Lang et al. 2006; Dolby et al. 2011) into the Variscan highlands in central Europe (Broutin et al. 1990; Doubinger et al. 1995; Dimitrova and Cleal 2007; Bashforth et al. 2011). These persistent species pools have been documented with autochthonous and allochthonous macrofossils, including transported charcoal, and with palynomorphs. They suggest resident high-elevation populations throughout the Variscan-Appalachian mountainous regions, perhaps outside of the regions subject to the highest amounts of rainfall during glacial-interglacial cycles but still within the area of moderate temperatures. The far western Pangean floras appear to have existed at all elevations, reflecting a general west-to-east gradient in moisture, particularly from the later Middle Pennsylvanian into the Permian. As summarized by Ziegler et al. (2002; fig. 5), walchian conifers are known from many sites in Euramerica but only a few outside of that area; thus, it is unlikely that populations of these plants resided permanently in eastern Pangea (Angara and Cathaysia) during drier periods.

The biogeographic distributions of seasonally dry plants are imperfectly understood (an understatement). The likelihood of their preservation as macrofossils is low, due both to their position on the landscape and to the climatic conditions under which the plants flourished (Gastaldo and Demko 2011). Consequently, we see only glimpses of them, even in palynological studies, which might be expected to capture these elements more commonly than macrofossils. Nonetheless, it is certain that one or more biomes, populated by plants tolerant of mild to extreme seasonal moisture deficits, existed continuously in the tropics along with the much better-known and better-documented wetland biome.

Climate models should play a significant role in helping us understand the patterns of distribution of the seasonally dry flora. Unlike the fate of the wetland biome during dry phases
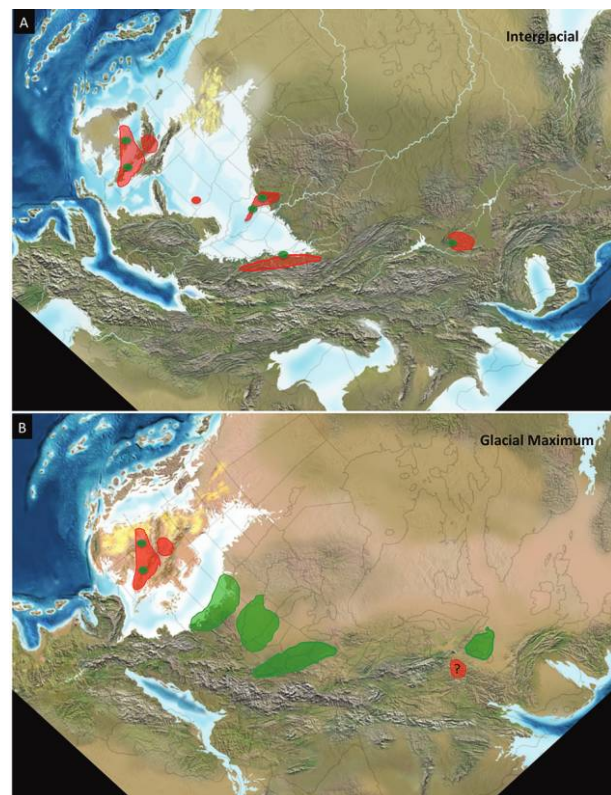

Fig. 20 Biogeographic patterns, Euramerica. Known occurrences of seasonally dry and wetland biomes during a glacial-interglacial cycle. The seasonally dry elements are shown in red. The wetland flora is shown in green. In areas of mixed floras, where it is presumed that seasonally dry conditions predominate, refugial pockets of wetland flora are indicated by small green ovals. The interglacial map is Pennsylvanian and the glacial map Early Permian (it was necessary to use the Early Permian map in order to show the sea in an off-continent position during glacial maximum), although the floras shown are Pennsylvanian. Base maps courtesy of Ron Blakey, Northern Arizona University.

of a glacial-interglacial cycle, the seasonally dry biome probably did not break up into isolated pockets or refugia during the wetter parts of cycles. Admittedly limited but nonetheless powerful evidence suggests that during the driest parts of glacial cycles, when vertic, sometimes calcic, soils were forming in basinal lowlands throughout nearly all of the cratonic interior of equatorial Pangea, the seasonally dry flora migrated into these areas and became the dominant vegetation in those basins (Falcon-Lang et al. 2009, 2011*b*, 2011*c*; Plotnick et al. 2009). By extension, this flora also was likely dominant in the low-latitude nonbasinal areas. These drier parts of cycles may have exceeded the wetter parts in terms of the overall time represented, which would mean that even though poorly represented in the fossil record, the seasonally dry biome may have been the dominant vegetation type of the Pennsylvanian tropics (Falcon-Lang et al. 2009). Additionally, if similar to the modern world, the near-tropical regions may have been more persistently seasonal than the equatorial tropics, meaning that there would have nearly always been large areas of sea-

sonally dry-wet climates throughout central Pangea within which these dryland floras could have resided permanently.

Discussion

The perception of the Pennsylvanian tropics as an ever-wet steaming jungle is a mistaken vision that is slowly loosening its grip on terrestrial late Paleozoic paleontology, even as it persists in the public mind. Climate modelers, sedimentologists, and stratigraphers have accommodated climatic variation into their work. Climatic factors exert a strong and sometimes primary control on sedimentation dynamics (Stanley and Warne 1994; Peizhen et al. 2001) and, even through climatic effects on erosion, greatly affect timing and rates of mountain building (Montgomery et al. 2001; Grujic et al. 2006; Whipple 2009). The long-recognized cyclic patterns of sedimentation in paleotropical regions were early attributed to glaciation in the Southern Hemisphere (Coleman 1908) and were appreciated by paleobotanists at the time (White 1907, 1909). Modern research on these subjects, as discussed above, has greatly refined our understanding of Ice Age history and dynamics. For the purposes of this article, it is most important to recognize, above all else, that there were regular and numerous changes in climate, sea level, and sedimentation patterns, driven proximately by changes in ice volume and its effects on atmospheric circulation. If CO_2 were the ultimate cause of the ice fluctuations, as models suggest, then the cause of oscillations in that variable remains opaque. The second point is that these changes in climate were accompanied by great changes in the spatial distribution of floras through time, a dynamic that should play as strongly into our thinking about evolution as it does about paleoecology. And, finally, it is the intention here to provide a somewhat more refined understanding of the details of where and when climatic changes of different types occurred within glacial-interglacial cycles and what the effects of those may have been on vegetational patterns. As a phenomenon with global expression, climatic changes should have enormous predictive power to help us understand floristic and associated physical geological changes, even in areas where the effects of sea level changes cannot be observed directly, such as within mountain belts.

Taphonomy, the processes and events attendant fossilization, is possibly the single greatest influence on perception of the Pennsylvanian tropics as a vast, static wetland. Quite simply, wetland vegetation is overwhelmingly more likely to be preserved, and beautifully so, than vegetation in seasonally dry habitats. The strong selection against preservation of organic matter in a dryland settings is, in general, a matter of three factors, as discussed in detail by Gastaldo and Demko (2011). These are amplified in important ways when considered in the context of the LPIA. The first factor, and the most important, is short-term burial by removal of the buried organic matter from oxygenic decay—its burial below the vadose zone of the water table. In periodically to perennially dry soils (forming under dry subhumid to arid climates), this is much less likely to happen than in wetlands, with high water tables, which can be present under any kind of climate (though climate is likely to dictate the areal extent of the wetlands). Thus, we should rarely expect to find seasonally dry floras, particularly if, as in the Pennsylvanian, they tend to occur in the falling stages

of sea level and early interglacial lowstands. These are times of dropping water tables and landscape erosion. Wetlands, on the other hand, are concentrated in mid- to late lowstand and early phases of transgression during Pennsylvanian glacial cycles. These are times when rising sea level creates ideal conditions for intermediate-term burial below a column of seawater. This intermediate-term burial, if organic remains can survive to this point, may allow sufficient time for long-term burial due to the tectonically driven creation of accommodation space in basinal areas. Dryland floras and wetland floras, within this framework of glacial-interglacial cycles, and their directly and closely related changes in climate, sea level, and sedimentation patterns have quite unequal chances of making it into the fossil record. Thus, the wetland signature overwhelms that of the drylands, which even though rarely and usually poorly preserved may have been an important part of and long resident in the Pennsylvanian lowlands (Falcon-Lang et al. 2009).

Roof Shales versus Peat-Forming Floras: Implications from Biogeography

The widespread occurrence of many elements of typical coal-basin roof shale floras (Gastaldo et al. 1995) beyond the geographic extent of coal-bearing strata suggests that clastic substrate floras do not provide a 1 : 1 representation of peat substrate floras, at least in dominance-diversity structure. It has sometimes been assumed that these two kinds of floras are interchangeable and one is fully reflective of the other (Jennings 1986). However, examination of the composition of peat substrate floras using coal balls (anatomically preserved peat stages of the coal; see summary in Phillips et al. 1985) demonstrates very different patterns of dominance from mineral substrate floras. There are few genera that can be confidently assigned to only one kind of substrate or the other (mineral or peat), though there may be many such species. It is difficult to detect species differences with confidence due to the very different forms of preservation between coal balls and adpressions (compressions and impressions; see Shute and Cleal 1986) and, hence, the different character suites on which much of the taxonomy is based. Direct comparisons are possible and have been made in some instances (e.g., pteridosperm foliage species [Oestry-Stidd 1979; Mickle and Rothwell 1982; Beeler 1983; Reihman and Schabilion 1985; Cleal and Shute 2012; Raymond et al. 2013], lycopsid stem taxa [Bateman et al. 1992; DiMichele and Bateman 1996]). However, comparisons at a broader level show consistent differences in quantitative aspects of composition, such as the more common occurrence of the lycopsid *Sigillaria* or the greater dominance of pteridosperms (King et al. 2011; Wagner and Castro 2011) in mineral substrate wetlands than in peat swamps. Some larger-scale patterns, such as the qualitative rise in importance of the marattialean fern clade in wetlands of the late Middle Pennsylvanian (Phillips et al. 1974; Pfefferkorn and Thomson 1982; Phillips and Peppers 1984; Peppers 1996; Dimitrova et al. 2005; Dimitrova and Cleal 2007) or the decline in wetland cordaitales (Phillips and Peppers 1984; Raymond et al. 2010), are detectable in both forms of preservation and appear to occur at approximately the same time in both, despite differences in quantitative aspects (for the rise in tree ferns, cf. Pfef-

ferkorn and Thomson 1984 and Phillips et al. 1985 or Peppers 1996; the timing is the same even though quantitative expression differs).

Also bearing on this matter are the discoveries of plants in small intermontane basins in the Variscan portions of the Central Pangean Mountains that contain unusual elements, particularly pteridosperms and ferns, related to but atypical of roof shale assemblages (Cleal 2008b; Šimůnek and Cleal 2011). Such finds imply that even among the largely humid-climate, wet substrate floras, there are differences that reflect habitat heterogeneity. Such appearances of odd members of various groups also have been reported from wetland-type floras in western regions of Pangea (Read 1934; Mamay and Read 1956; Tidwell et al. 1988; Knaus and Lucas 2004; DiMichele et al. 2013b), though many of these floras also contain seasonally dry elements.

Dry Floras: Uplands versus Climate

The most persistent misconception about plants from seasonally dry habitats is that they are unfailing indicators of uplands. As reviewed above, this reflects the underlying supposition that under a common, presumably wet climate, slope and elevation are both necessary and sufficient to create the conditions under which these dry-habitat plants are favored and where the lowland wetland plants cannot live. When considering the occurrences of these dry-habitat plants in the vast expanses of the west-central Pangean interior, where there were no mountains within thousands of kilometers, it became necessary either to propose phantom uplands or to require that small amounts of elevation were sufficient to support dry substrate plants in the midst of the soggy bottomlands (Cridland and Morris 1963). Spatiotemporal, biogeographic patterns also conflict with upland models. Read and Mamay (1964), for example, suggested that climate was drier in the western United States earlier than in the east during the Pennsylvanian, based on the small numbers of wetland floras known from the western parts of Pangea and their concentration in the Early Pennsylvanian, in combination with early occurrences of dryland plants of various kinds in the west and their later appearances in the east. Uplands play no role in such an explanation because there were not systematic changes in elevation from west to east within that time and space. Pfefferkorn (1980) and Winston (1983) also recognized that dry and upland were not necessarily interchangeable concepts. Gastaldo (1996), Šimůnek (2008), and Opluštil et al. (2013a) all make strong cases for climatic control of biomic dynamics, even in intermontane regions of central Pangea, and conclude that they reflect the same kind of climate cycles that are found in lowland basins.

Can elevation alone (drainage), under uniformly humid climate, account for occurrences of the dryland flora? It must be emphasized that cyclic patterns of lithological change, though without any evidence of marine influence, can be detected in intermontane regions (Cecil 2013; Opluštil et al. 2013a, 2013b). These lithological sequences document changes in prevailing climate similar to those in more classic cyclothems of the paralic regions in west-central equatorial Pangea—specifically, the alternation of seasonal subhumid to semiarid climates with humid climates on the time frame of glacial-interglacial cycles. This strongly suggests the existence of an external allocyclic cause, paralleling that seen in marine-influenced basins where the consequences of sea level rise and fall are more apparent. Although tectonic effects may overprint cyclicity, that lithological cyclicity can still be recognized is a significant indicator of the importance of climate.

However, if one were to push aside the physical indicators of glacially driven climate changes in tectonically active areas with steep elevational gradients, the following questions might be asked: Does evidence suggest that elevation alone, under a constant, humid background climate (which is necessary to form peat/coal any time or place other conditions permit) is sufficient to explain occurrences in basins (presumably via long-distance transport) of cordaitaleans, conifers, and other taxa otherwise atypical of wetland assemblages? Is it reasonable to assume that slopes alone will create enough soil drainage to result in periodic or nearly continuous moisture stress and that such soil drainage will be the sole factor setting these habitats and their floras apart from low-lying bottomlands, again under invariantly humid background climate? In other words, are drylands set apart from wetlands simply due to the effects of soil drainage, were climate to be held constant as humid/perhumid? Note that one must make an explicit assumption about the climate mode because low-ash peat (as a parent material to economic coal beds), which is part of these landscapes, will not form under climates with high seasonality of rainfall. The answer to all these questions, in brief, appears to be no. A more subtle interpretation, however, would suggest that elevation, if high enough to engender climatic and associated microclimatic changes, might have such effects, though such elevation would have to be considerable in the tropics.

There are opportunities to assess empirically the contribution of elevational heterogeneity to total diversity in Pennsylvanian basinal lowlands. Several reports from within the Variscan mountain belt in central Europe describe narrow, steep-sided valleys with coal at the elevation of the valley floors, possibly at base elevations of 1000 m or more (Opluštil 2005). Clastic deposits associated with the coals contain floras that appear to reflect wet climates. These floras are drawn almost entirely from wetland evolutionary lineages, even if some species and genera of pteridosperms and ferns are rarely found in typically lowland wetland settings from the interior Pangean and marginal-Variscan flatlands (Cleal 2008b; Šimůnek and Cleal 2011). It has been hypothesized that the steep walls of these narrow basins supported a flora that, though adapted to wet climates, was specialized for growth under conditions of less waterlogging than found in the basin floors, where coals developed (Opluštil and Cleal 2007). These assemblages, however, lack elements typical of the seasonally dry flora, mainly conifers or known minor associates of the dominant elements. Similarly, Wagner and Álvarez-Vázquez (2010; and, by default, Bashforth et al. 2010) note the paucity of conifers in Late Pennsylvanian Iberian Peninsula floras, despite the presence of abundant well-drained mountainous habitats, including high-elevation alluvial fans, in proximity to basinal environments. On a smaller scale, Feldman et al. (2005) contrast several examples of Late Pennsylvanian valley fills from late interglacial to early glacial time periods. Those that are deep and reflect large drainage basins, high rainfall, and high water throughput lack conifers. In contrast, shallow valleys

reflective of small drainage basins that formed under more strongly seasonally dry climates (corroborated by the characteristics of time-equivalent paleosols and sedimentology) contain floras dominated by xeromorphic taxa, often including a much larger spectrum of characteristic seasonally dry plants. Thus, again, where there is evidence of significant topography, the dominant dryland elements are found only where and when there is additional evidence of climatic seasonality of moisture.

Such patterns suggest that, much like the modern tropics, under conditions of high rainfall of a nearly aseasonal to weakly seasonal pattern, slope and drainage effects are reduced in importance as agents of habitat differentiation (e.g., British peat lands; Moore 1987). In modern tropical wet forests under climatic regimes where rainfall exceeds evapotranspiration for most of the year, accompanied by only a limited dry season (humid to perhumid climates in the terminology of Cecil and Dulong 2003), effects of elevational heterogeneity are suppressed and found not to contribute significantly to landscape-level (beta) biodiversity (Davidar et al. 2007). Rather, the main control on beta diversity appears to be variation in the seasonality of rainfall and hence the number and length of periods of drought across a landscape, to which most tropical trees are highly sensitive (Davidar et al. 2007; Engelbrecht et al. 2007). Gradients in seasonality of rainfall contribute to increases in beta diversity under such conditions. Seasonal moisture stress, however, will reduce site (alpha) diversity at any given point even as it creates regional diversity gradients.

Changes in dryland flora through time—what happened to the cordaitalean-dominated assemblages? Cordaitaleans were the unquestionable monarchs of the seasonally dry tropics from the Mississippian to the mid–Middle Pennsylvanian (Falcon-Lang and Scott 2000; Falcon-Lang and Bashforth 2005; Šimůnek 2008), often accounting for >75% of the biomass in many assemblages (Falcon-Lang 2003b). They were accompanied by an interesting array of other seed plants. The whole system gradually diminished during the later Middle Pennsylvanian, and its frequency tapers off considerably in the Late Pennsylvanian. Šimůnek (2008) notes that these floras are not found in environments that appear to be semiarid but rather are associated with floras and physical environments that appear to be humid, perhaps trending to subhumid (Opluštil et al. 2005). After considering a large number of recorded occurrences of cordaitalean-dominated seasonally dry floras, Bashforth et al. (2014) conclude, in agreement with the above authors, that cordaitaleans occupied seasonal but relatively humid environments.

Conifers, on the other hand, are often found, even in their earlier parautochthonous occurrences (Plotnick et al. 2009), in association with settings that appear to have been more seasonally dry than those in which cordaitaleans were dominant. Conifers, via pollen occurrences, are suspected to have appeared in the late Mississippian (Turner et al. 1994; Falcon-Lang 2006), but they do not really become important parts of equatorial floras until the Late Pennsylvanian, where there are numerous occurrences throughout Euramerica, as discussed above. Conifers also are associated with a wide array of other kinds of seed plants, often with considerably xeromorphic foliar morphologies. Many conifer-containing assemblages are dominated or codominated by these other kinds of plants, such as callipterids. This is in contrast to the cordaitalean assemblages where the minor constituents rarely are prominent elements quantitatively, in terms of biomass. Where such occurrences do occur, they often are on substrates that suggest strong edaphic controls, such as floras containing abundant *Megalopteris* or *Lesleya*.

These patterns of gradual transition from cordaitalean to coniferalean dominance as the major seasonally dry biome correlate with a gradual drying trend in the tropics through the late Middle Pennsylvanian and Late Pennsylvanian. These independently determined climatic trends reveal spreading seasonality in the tropical realm. This seasonality becomes apparent even during the wet phases of glacial-interglacial cycles beginning near the Desmoinesian/Atokan (Bolsovian-Asturian) boundary, revealed by changes from ombrotrophic domed peats to rheotrophic planar peats (Cecil 1990), associated with increases in coal sulfur (Cecil et al. 1985; Neuzil et al. 2005) and with changes in sandstones, indicating a transition from wet low-seasonality climates to greater seasonality (Bertier et al. 2008). The wetland flora also undergoes many compositional and dominance-diversity changes at this same time (Pfefferkorn and Thomson 1982; Phillips and Peppers 1984; Peppers 1996), much more abruptly than the seasonally dry flora.

Ecological and Evolutionary Implications

Consideration of climate, but within a glacial-interglacial, oscillating context, has many profound implications for understanding vegetational dynamics and for possible controls on evolutionary patterns. We will touch on two here.

Periodic reassembly of the wetland biome versus spatial migration of the seasonally dry biome. Analysis of the wetland biome, particularly that of peat-forming landscapes, indicates a considerable amount of conservatism in species composition and dominance-diversity structure through millions of years and multiple glacial-interglacial cycles. This assessment has been based on both macrofossils and microfossils recovered from successive coal beds (Phillips et al. 1985; Willard and Phillips 1993; DiMichele and Phillips 1996b; Peppers 1996; Pfefferkorn et al. 2000, 2008; DiMichele et al. 2002; Willard et al. 2007), representing the wettest parts of glacial-interglacial cycles. It appears, furthermore, to be undergirded by considerable phylogenetic conservatism in the resource centroids of the major clades, resulting in phylogenetically conservative patterns of species replacement through time (DiMichele and Phillips 1996a), so-called niche conservatism (this is currently an active field of study; see Ackerly 2003; Wiens 2004; Wiens and Graham 2005; Wiens et al. 2010). Niche conservatism is particularly important here because of the much lower diversity of the late Paleozoic, in general, than of the modern. We are used to thinking of large amounts of heterogeneity and strongly individualistic responses of species to changing climates and physical conditions in the modern world (Jackson 2006; Mascaro et al. 2013), and no doubt this is so at some spatiotemporal scale. However, there do seem to be biomic bounding conditions, set by large-scale climatic effects and physiography, and this can be quite clearly discerned in the less cluttered world of the Paleozoic. When niche conservatism is considered, the marked clade-by-environment patterns of species replacement through time suggest that, as proposed by Wiens (2004; see also Kozak and Wiens 2006), niche conser-

vatism may promote speciation by restricting and fragmenting species distributions during times when their favored habitats become aerially restricted.

Recurrence of similar wetland dominance-diversity patterns from one period of humid/perhumid climate to the next most likely requires reassembly of this vegetation, given the indications that these floras became strongly constricted to refugia during the dry portions of climate cycles. The exact pathways of reassembly are most likely dictated first by the dispersal capacities of the various species and second by the capacity of these species to survive under the limited-nutrient, long-flooded conditions found in Pennsylvanian wetlands. It may be that this latter capacity, in particular, favored the repeated reexpansion of the arborescent lycopsids, many of which had large but floatation-equipped, seedlike dispersal units (*Lepidocarpon*, *Achlamydocarpon*; Phillips 1979) and specialized physiologies favoring growth under highly stressed, flooded conditions (Green 2010). That same flooding, in contrast, may have suppressed the expansion of the marattialean tree ferns, which were equipped, it would appear, with much higher dispersal capacities, via their billions of small isospores, possibly more rapid attainment of sexual maturity (cheap construction compared to a lycopsid tree, many of the latter having monocarpic growth habits as well), but also a requirement for a suitable place for growth and sexual reproduction carried out by a surficial gametophytic prothallus. Despite beginning to increase in abundance in the Middle Pennsylvanian, it was not until catastrophic environmental changes eliminated the lycopsid hegemony, near the Middle–Late Pennsylvanian boundary, that the tree ferns rapidly expanded to dominance in wetlands.

In contrast to these kinds of dynamics, seasonally dry floras appear to have maintained large standing crops of trees and associated smaller plants in many parts of the Pangean tropical belt, even during the least favorable times for them, when humid climates and wetlands were widespread. This is true of both the earlier cordaitalean-dominated forests and the later conifer-dominated woodlands, with their associated callipterids, taeniopterids, and cordaitalean-forest holdovers. Evidence of the continued existence of these plants during what were the wetter periods in the coal basins is suggested by both the presence of coniferophytes in western Pangea seemingly at all times from the late Middle Pennsylvanian onward and their presence in the mountainous regions of central Pangea, revealed mainly by pollen. In the same way, cordaitaleans, which may have been less tolerant of severe drought than the conifers and more tied to mesic habitats, are revealed by both pollen and macrofossils during what appear to be the wetter parts of glacial-interglacial cycles. Interpreting the palynological record of cordaitaleans is problematic because of the conservatism of their pollen morphology and the great breadth of ecological preference encompassed by the clade.

As a consequence of the large acreage evidently occupied by the seasonally dry biomes during their respective times of tropical maxima and minima, their spatiotemporal patterns appear to be controlled largely by expansion and contraction of populations across the area of favorable habitat. During such periods of expansion and contraction, most of the species that made up these ecosystems likely maintained continuity of large panmictic populations, given almost certain wind-pollinated life histories. This is quite a different pattern from that proposed for the wetlands, one of significantly greater organizational conservatism. As yet unpublished data of W. DiMichele and colleagues, mainly from the western parts of Pangea, suggest that these species assemblages did not show any noteworthy changes during times of significant climatic change at either the Atokan-Desmoinseisan boundary or the Middle–Late Pennsylvanian boundary.

Furthermore, the change from cordaitalean dominance to conifer dominance appears to have taken place gradually, as well. Thus, one might think of these assemblages as buffered against catastrophic changes by their large population sizes, capacities to tolerate moisture stress (and temperature stress (?), given their mountainous distributions in some areas), availability of migratory routes, and K-selected reproductive modes.

Evolutionary implications of plant ecologies × climate fluctuations. The potential for isolation of populations, wetland or seasonally dry, during parts of glacial-interglacial cycles may have been a powerful engine of evolutionary change. This will manifest itself in different ways for populations of seasonally dry and wetland plants. All of the dominant seasonally dry plants were wind-pollinated seed plants, and most of the less common forms also were seed plants. Wetlands, by contrast, were dominated by a broad spectrum of both homosporous and heterosporous lower vascular plants and various kinds of primitive seed plants, which, whereas mainly wind pollinated or dispersed, may also have been obligately tied to water for reproduction or dispersal. Thus, these two floras possibly had different average patterns of dispersal limitation that affected their evolutionary patterns differently. That said, there also are many life-history similarities among the dominant elements of these two kinds of floras. The most prominent of these similarities is the small size and dispensability of the microspore/isospore phase of their life histories. Also similar is the gigantic, apparently continuous, distributions of these plants during the respective climate phases of glacial-interglacial cycles favorable to each.

Wetland plants, as discussed by Falcon-Lang and DiMichele (2010), ought to have been strongly influenced by the periodic confinement to refugial wetlands during interglacials through early glacial maxima. This is primarily due to the reduction or elimination of many dispersal pathways, potentially restricting gene flow, thus creating conditions for the evolution of new species in small, isolated populations. Such restrictions certainly became more severe and the isolation of populations ever greater during the later Middle Pennsylvanian (Desmoinesian) and early Late Pennsylvanian (Missourian), when much evidence indicates increasing aridity in the tropical realm (wets less wet, drys more dry), possibly tied to extensive melting of polar ice (Fielding et al. 2008; Rygel et al. 2008). In the midst of this interval, there is a great turnover in the flora, accompanied by the loss of most of the dominant Middle Pennsylvanian lycopsids (Phillips et al. 1974; Heckel 1991*a*), a change in the common tree ferns (Lesnikowska 1989), and many changes in the pteridosperm component of wetlands (Phillips 1981; Phillips and Peppers 1984; DiMichele et al. 2006*a*; Wagner and Álvarez-Vázquez 2010). From a life-history viewpoint, perhaps the least likely to produce new species during these periods of habitat contraction and isolation were the arborescent lycopsids. Most of these heterosporous plants

produced large volumes of highly dispersible microspores, which often are abundant even in strata deposited during the drier periods (Turner et al. 1994; Falcon-Lang et al. 2009; Hawkins et al. 2013). The near disappearance of these plants at the Middle–Late Pennsylvanian boundary thus may reflect a particularly severe period or series of sequential intervals of intense fragmentation of their populations (Phillips and Peppers 1984; Heckel 1991a). Tree ferns similarly may have been considerably insulated from founder effects during periods of population contraction due to both their prolific production of small isospores and the subsequent high dispensability of these spores (Lesnikowska 1989; Millay 1997). At the other end of the spectrum were the medullosan pteridosperms. These plants had some of the largest pollen grains in seed plant history, which begs the question of animal pollination (Taylor 1978; Taylor and Millay 1979). Experimental analysis of this type of pollen indicates little likelihood of wind delivery (Schwendemann et al. 2007). In an interesting twist on this matter, Peter Crane (personal communication) hypothesized that the medullosans may have had life histories similar to those of heterosporous plants, wherein their pollen was water dispersed and swimming sperm reached ovules without delivery of pollen to a pollen chamber. Such a life history would be very different from that of the lycopsids, because neither the microspore nor the seed/dispersal organ is particularly suited to wide dispersal, effectively permitting high levels of speciation in response to isolation. In keeping with the size proportions of their pollen grains, medullosan seeds are the largest of the Pennsylvanian tropical flora (Sims 2012) and may have floated, like small coconuts (Falcon-Lang 2009 has suggested a mangrove habit for *Macroneuropteris scheuchzeri*), or required animal vectors for dispersal (many have fleshy sarcotestas, which may have attracted animals, and thick sclerotestas, which may have resisted crushing and passage through the gut). Despite many synthetic studies of these plants, however, including paleoecology, biogeography, and phylogentic relationships (Phillips 1981; Stidd 1981; DiMichele et al. 2006a; Hilton and Bateman 2006; Hilton and Cleal 2007; Cleal 2008b), there appears to be only one study, that of Raymond and Costanza (2007), that investigates species durations of medullosans and compares them to those of other groups; these authors find that, indeed, medullosan species have shorter durations than wind-pollinated wetland cordaitalean or callistophytalean seed plants.

There are reasons to expect that the effects of glacial-interglacial climate changes on dryland flora may have been qualitatively different from those of the wetlands, but this too has not been investigated, and such investigation may be more challenging than for wetland plants because of the poor preservation of tropical dryland species during the Pennsylvanian, limiting understanding of species-level spatiotemporal patterns. Nonetheless, there are interesting patterns worth noting that prompt some speculation. Most of the dryland plants were wind pollinated. Studies of modern wind-pollinated plants subject to isolation in fragmented landscapes suggest high levels of gene flow created by pollen dispersal. Documentation of this pattern in conifers (Jørgensen et al. 2002; Liepelt et al. 2002; O'Connell et al. 2007) may have the most applicability to the late Paleozoic, where the two dominant groups in seasonally dry habitats, cordaitaleans and conifers, are both con-

iferophytes in a broad evolutionary sense (Hernandez-Castillo et al. 2001b; Rothwell et al. 2005; Looy 2007). High gene flow might be expected to have kept speciation rates low in these groups, regardless of fluctuating climates. However, recent studies of both cordaitaleans (Šimůnek 2000, 2007; Raymond et al. 2010) and conifers (Rothwell et al. 1997; Hernandez-Castillo et al. 2001b, 2009) indicate greater species numbers than previously appreciated. This can be considered from a life-history perspective. Both cordaitaleans and primitive walchian conifers have large pollen grains of primitive architecture compared to more advanced groups of conifers (Gomankov 2009), generally produced in simple pollen cones (Mapes and Rothwell 1998). Compound cones, paralleling ovulate structures in organization, also have been found (Hernandez-Castillo et al. 2001a). Additionally, these early groups have much simpler ovulate cone architectures than modern conifers (Florin 1951; Mapes 1987; Kerp and Clement-Westerhof 1991; Hernandez-Castillo et al. 2001b), which may have given them much less efficient pollen capture than modern groups with compact cones (Niklas 1985; Owens et al. 1998). In addition, pollen morphology appears to track the patterns of ovulate cone evolution (Gomankov 2009). Thus, one might speculate that in these primitive coniferophytes, given the periodic isolation of their populations, particularly in the mountainous regions of central and western Pangea, restriction of gene flow may have been more likely than in modern groups. Perhaps paralleling the patterns found in other wind-pollinated or wind-micro/isospore-dispersed Pennsylvanian taxa, these primitive wind-pollinated plants may have had higher rates of speciation than those seen in modern coniferophytes subject to periodic isolation during the present ice ages.

Conclusions

The Pennsylvanian ice age provides an excellent point of comparison to our modern period of cool Earth climate, each dominated environmentally by the framework of glacial-interglacial cyclicity. Differences from today in the composition of the terrestrial biota and the diversity of that biota make the LPIA world a place within which to look for generalities about ecological and evolutionary dynamics, otherwise formulated on the basis of our thin, modern slice of time (extended back a bit into the Pleistocene).

Long study of the late Paleozoic tropical realm leads me to a number of (unsurprising) conclusions.

1. Environmental change, often of a catastrophic, cataclysmic, or just plain old really rapid nature, happens often. Such change seems to give little in the way of warning, at least on the spatiotemporal scales detectable by paleontological resolution, suggesting the existence of biotic thresholds. The crossing of such thresholds leads to so-called regime shifts, which are rapid and often irreversible. Furthermore, change of smaller-scale similarly is the rule rather than the exception.

2. The late Paleozoic tropics were characterized by a number of distinct biomes, divisible principally into a humid to perhumid wetland group and a subhumid to semiarid dryland group. Each of these has a great deal of variability, reflecting habitat preferences and the vagaries of dispersal limitations and incumbency.

3. Plants of the late Paleozoic reflected climate closely and faithfully, much like they do today.

The Pennsylvanian Coal Age tropics were not wet. They alternated between wet and dry with each glacial-interglacial cycle. The degree of development of either of these climate extremes varied from one cycle to the next, but a long-term trend of drying and warming is suggested.

4. The evolutionary dynamics of the wetland and seasonally dry species pools were different. The difference reflects the periodic contraction into and expansion from refugia of the wetlands within the tropical belt versus the persistent widespread, highly connected habitats occupied by the dryland species in western and parts of central Pangea.

Acknowledgments

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