

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

International Journal of Coal Geology

journal homepage: www.elsevier.com/locate/ijcoalgeo

Cyclic changes in Pennsylvanian paleoclimate and effects on floristic dynamics in tropical Pangaea

William A. DiMichele^{a,*}, C. Blaine Cecil^{a,b}, Isabel P. Montañez^c, Howard J. Falcon-Lang^d^a National Museum of Natural History MRC-121, Smithsonian Institution, Washington, DC 20560, USA^b U.S. Geological Survey, Reston, VA 20192, USA^c Department of Geology, University of California, Davis, CA 95616, USA^d Department of Earth Sciences, Royal Holloway, University of London, Egham, Surrey TW20 0EX, UK

ARTICLE INFO

Article history:

Received 17 March 2009

Received in revised form 12 January 2010

Accepted 12 January 2010

Available online 20 January 2010

Keywords:

Upland flora

Conifers

Cordaitaleans

Coal

Paleosol

Glaciation

ABSTRACT

Wetland floras narrowly define perceptions of Pennsylvanian tropical ecosystems, the so-called Coal Age. Such wetlands reflect humid to perhumid climate, leading to characterizations of Pennsylvanian tropics as everwet, swampy. These views are biased by the high preservation potential of wetlands. Sedimentation patterns, paleosols, and fossil floras indicate the presence of vegetation tolerant of subhumid to dry–subhumid, perhaps semi-arid climate in basins between peat formation times. Understanding the significance of this seasonally-dry vegetation has suffered from conceptual and terminological confusion. A clearer view has emerged as models for framing the data have improved. Basinal floras typical of seasonally-dry conditions, relatively low soil moisture regimes, are well documented but mainly from isolated deposits. Some of the earliest, dominated by primitive pteridosperms (“Flözfern” floras), occur in clastic rocks between European Early Pennsylvanian coal beds. Later Early Pennsylvanian, fern–cordaitalean vegetation, different from coal floras, is preserved in marine goniatite bullions. Conifers are first suggested by late Mississippian *Potoniesporites* pollen. About the same time, in North America, broadleaf foliage, *Lesleya* and *Megalopteris* occur in basin-margin settings, on drought-prone limestone substrates. The best known, xeromorphic floras found between coal beds appear in the Middle through Late Pennsylvanian, containing conifers, cordaitaleans, and pteridosperms. The Middle Pennsylvanian appearances of this flora are mainly allochthonous, though parautochthonous occurrences have been reported. Parautochthonous assemblages are mostly Late Pennsylvanian. The conifer flora became dominant in western and central Pangaeian equatorial lowlands in earliest Permian. Location of the humid–perhumid wetland flora during periods of relative dryness, though rarely discussed, is as, or more, perplexing than the spatial location of seasonally-dry floras through time – wetland plants had few migratory options and possibly survived in small refugia, within and outside of basins. Coupled oscillations in climate, sea level, and vegetation were driven most likely by glacial–interglacial fluctuations, perhaps controlled by orbital cyclicity.

Published by Elsevier B.V.

1. Introduction

The Pennsylvanian Subperiod of the Carboniferous is often referred to as the “Coal Age” in recognition of its vast deposits of European and North American coal. Over a period of 15–20 million years, wetland landscapes, some of which appear to have been of vast aerial extent (Wanless and Wright, 1978; Cecil et al., 2003a; Greb et al., 2003) formed at low latitudes during cyclic oscillations of climate and attendant sea level (Cecil, 1990; Cecil et al., 2003a; Poulsen et al., 2007), driven, at least in part, by glacial–interglacial cyclicity (Wanless and Shepard, 1936; Heckel, 2008; Rygel et al., 2008). The excellent

quality of many of the resultant low-ash coals, especially during the Early and early Middle Pennsylvanian (for terminology used in this paper see Fig. 1), indicates derivation from domed, ombrogenous peat that was subjected to little if any influx of mineral matter (Cecil et al., 1985). Such peats form in the tropics today only under conditions of high rainfall, exceeding evapotranspiration for 11–12 months a year (humid to perhumid climate: Cecil, 2003; Cecil and Dulong, 2003). The relatively high-ash, high-sulfur coal beds of the late Middle and Late Pennsylvanian in North America were derived from planar topogenous peat (Cecil et al., 1985), under mildly seasonal climates, but sufficient to support an elevated water table. In either case, commercial-grade, high quality coal beds are *prima facie* evidence of humid climates. The Pennsylvanian flora of such ecosystems is well known from more than 150 years of study of pollen and spore microfossils and of macrofossils preserved in coal-ball concretions (e.g., Hooker and Binney, 1855; Phillips et al., 1985; Peppers, 1997).

* Corresponding author. Department of Paleobiology, National Museum of Natural History MRC-121, Smithsonian Institution, Washington, DC 20560, USA. Tel.: +1 2026331319; fax: +1 2027862832.

E-mail address: dimichel@si.edu (W.A. DiMichele).

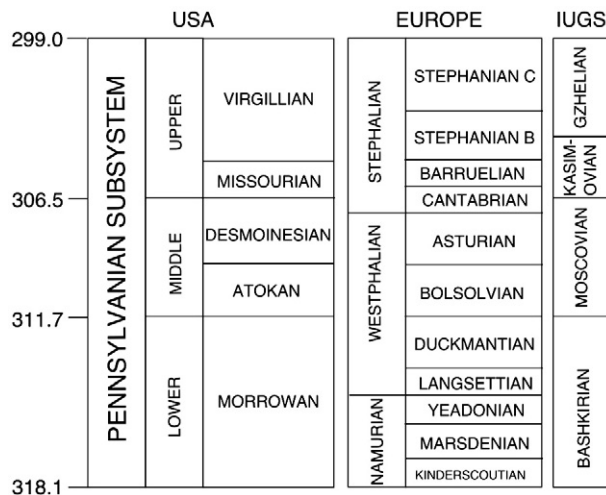


Fig. 1. Stratigraphic nomenclature of the Pennsylvanian Subperiod.

Reference is made to ancient non-marine wetlands throughout this paper. Terms used to define the characteristics of such wetlands remain ambiguous and/or vaguely synonymous. To overcome this, ancient wetlands are defined herein on the basis of the following: 1) materials that were deposited or formed in wetlands such as peat, limestone, or clastic minerals; 2) water source, mainly from rainfall (ombrogenous peats) or fluvial/ground water (topogenous peats); and 3) surface morphology of peat deposits, either domed or planar (Cecil et al., 1985). The use of the term “peat” is restricted herein to plant-derived organic deposits that originally contained $\leq 10\%$ mineral matter on a dry basis (Cecil and Dulong, 2003), which, following concentration in response to compaction and coalification to bituminous rank, resulted in coal ($< 20\%$ mineral matter). *Wetlands* are referred to by that term or by the term *swamp*, the latter especially to describe non-marine wetlands where either peat formed (peat swamp, $\leq 10\%$ mineral matter) or clastic materials were deposited (clastic swamp) under a vegetation that included trees. *Swamp* is defined by the United States Geological Survey as a “forested low, spongy land generally saturated with water and covered with trees and aquatic vegetation; may be a deepwater swamp..., which has standing water all or part of the growing season or ... forests that are only flooded periodically” (URL: <http://www.nwrc.usgs.gov/fringe/glossary.html>). The term has been extensively used to describe modern clastic swamps such as the “back swamps” of fluvial systems, peat-forming environments, such as the Okefenokee Swamp of Georgia, USA (topogenous, planar peat), or the peat-swamp forests of equatorial Southeast Asia (ombrogenous, domed peat) (Anderson, 1964; Cecil et al., 1985). Swamp includes small to vast wetland areas that are composed of either peat or clastics. The term swamp is used in preference to *mire* because early use of *mire*, which continues to persist, refers to small wet areas of nonspecific composition, but specifically excluding trees. The term *mire* is defined by the European Nature Information System as including “habitats that are saturated, with the water table at or above ground level for at least half of the year, dominated by herbaceous or ericoid vegetation e.g., bogs, marshes. Includes waterlogged habitats where the groundwater is frozen. Excludes waterlogged habitats dominated by trees or large shrubs” (URL: <http://glossary.eea.europa.eu>). The EUNIS terminology unites mire, fen, and bog.

Pennsylvanian-age coal beds often are intimately associated with fossil-plant-bearing siliciclastic rocks (mudstone, shale, siltstone, and sandstone) forming the immediate “roof shales” or subjacent mudstones in gradational contact with the coal bed (Gastaldo et al., 1995). In most cases, the floras of these rocks are composed of the same families and genera as those of the coal beds but of different

species in different proportions. These siliciclastic strata represent a wide range of lowland wetland environments, from the initial and final phases of swamp development (Gastaldo et al., 2004; DiMichele et al., 2007; Gastaldo et al., 2009), to riparian and fluvio-deltaic floras of various types (Scott, 1978; Gastaldo et al., 1995). Based on their similarity to peat-forming floras, these paraautochthonous to allochthonous floras in siliclastic deposits also grew under conditions of high rainfall, although probably in subhumid climates with some seasonal dryness (Cecil, 1990; Cecil and Dulong, 2003; Fielding et al., 2009). Consistent with this interpretation is the much greater geographic extent of such floras than of coal beds. Paleogeographically, coal-bed distribution is fully subsumed within the greater areal distribution of wetland siliciclastic, plant-bearing deposits. Consequently, successions of such wetland floras are well known from places where coal beds are rare, poorly developed or absent (such as New Mexico: Herrick, 1904; Read and Mamay, 1964). These low latitude, wetland, siliciclastic floras, in combination with the coal beds, indicate nearly continental-scale and long-persistent periods of relatively high rainfall and low evapotranspiration, with rainfall exceeding seasonal dryness for a minimum of 3–4 months a year, the humid to moist-subhumid climates of Cecil (2003).

Much of the Pennsylvanian was, however, a time when the Earth was experiencing intense polar glaciations on the developing Pangaea supercontinent (Fig. 2), particularly in the Southern Hemisphere (González, 1990; Fielding et al., 2008). The amount of ice appears to have varied on several different time scales, perhaps in keeping with orbital cyclicity and as yet incompletely understood changes in atmospheric pCO_2 concentrations (Montañez et al., 2007). As part of these coupled climate/sea-level fluctuations, tropical regions experienced more than simply eustatically driven sea-level changes and the alternation of marine and terrestrial conditions. They were alternately the home of climates that cycled between subhumid–humid–perhumid conditions and seasonally-dry-to-arid conditions (see Cecil et al., 2003a for terminology; also - Cecil, 1990; Feldman et al., 2005; Poulsen et al., 2007; Peyser and Poulsen, 2008), and the vegetation that accompanied these climatic changes (Falcon-Lang, 2004a).

Although coal beds record the most humid climates, there are a wide variety of other kinds of deposits between the coal beds, diagnostic of seasonal dryness, conditions quite different from those under which peats formed (Besly and Fielding, 1989; Cecil, 1990). Some of these are non-marine limestones, calcic Vertisols, and evaporites, known from modern environments in which evaporation exceeds freshwater influx or rainfall for many if not all months of the year. Furthermore, unlike the coal beds that are underlain by or laterally equivalent to paleosols that only form under a humid climate (Spodosols, Ultisols or Oxisols), many non-marine limestones can be traced laterally directly into calcic Vertisols, diagnostic of seasonal moisture deficits. These kinds of patterns record major cyclic shifts in sedimentary geochemistry from alkaline conditions during periods of limestone and calcic soil formation to acidic conditions during peat formation. Such shifts in sedimentary geochemistry have been attributed to climate change (Cecil, 1990). Paleosols also document a range of climatic conditions from those where rainfall exceeded evaporation to conditions of rainfall seasonality (Besly and Fielding, 1989; Falcon-Lang, 2004b; Driese and Ober, 2005). Furthermore, in strata occurring between the coal beds, and at a variety of geographic locations throughout the Pangaea equatorial region (Fig. 3), floras are known that clearly differed in composition from those of the wetlands (see additional references cited, and primary data in: Broutin et al., 1986; Lyons and Darrah, 1989; Broutin et al., 1990; DiMichele and Aronson, 1992; Galtier et al., 1992; Gastaldo, 1996; Falcon-Lang, 2003a; Falcon-Lang et al., 2009; Plotnick et al., 2009).

Thus, the dilemma: the Coal Age was also the age of one or more seasonally-dry, lowland vegetation types. These are not as well known as those of the wetter climates. For one thing, they are much

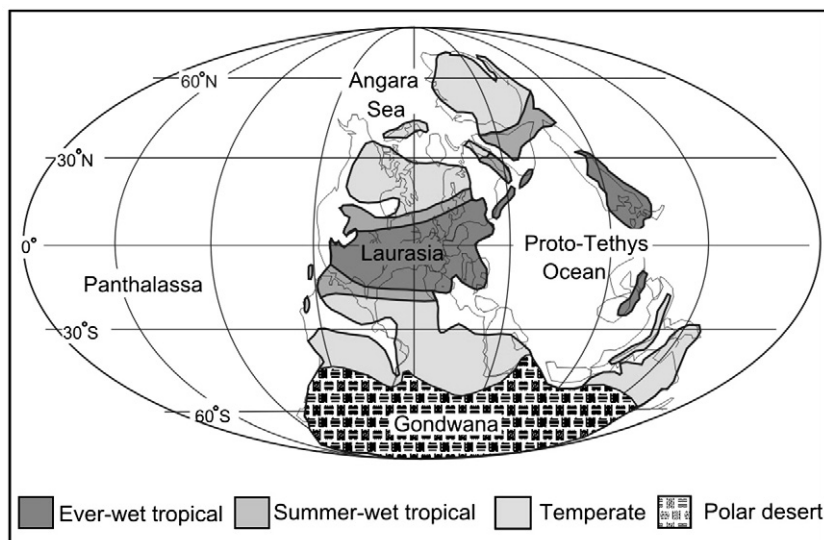


Fig. 2. The Pangaeen continent, major oceanic regions, and climatic belts during the time of glacial–interglacial cycles when wetlands predominated in the equatorial basinal lowlands.

more rarely preserved because plant remains are readily oxidized in dry soils. And secondly, targeting of Pennsylvanian-age coal beds by commercial mining has created vast exposures containing elements of the wetland flora, along with many opportunities for collecting. These collections fill the specimen cabinets of museums and universities throughout the world. However, drought-tolerant vegetation may have occupied all or part of the equatorial lowlands for as long, or perhaps even longer, than that of the wetlands, during any given glacial–interglacial cycle.

Pennsylvanian-age floras from seasonally-dry habitats have been known for many years, and some are well documented. There has, however, been a persistent misunderstanding of their spatiotemporal distribution, especially their place as important occupants of the basinal lowlands (Pfefferkorn, 1980; DiMichele et al., 2008). This has

led to a plethora of terms, such as “upland floras,” “extrabasinal floras,” “hinterland floras,” “The Mesophytic Flora” and “Flözfern,” most, implicitly or explicitly, linking the plants to “better-drained” soils and/or soils developed well above sea level and outside of the depositional systems. However, we only know them from the deposits within basins. These floras are, indeed, indicators of soil moisture deficits. They could have occurred anywhere climate created such conditions. The same applies to the opposite climate conditions. Thus, under humid–perhumid conditions, peat and other wetland vegetation can blanket even upland landscapes or, at least, grow well above base-level. This occurs today under the maritime climate in parts of Great Britain and New Zealand, where peat deposits blanket landscapes because high moisture input and a humid climate damp out some of the altitudinal effects on drainage as well as small surface

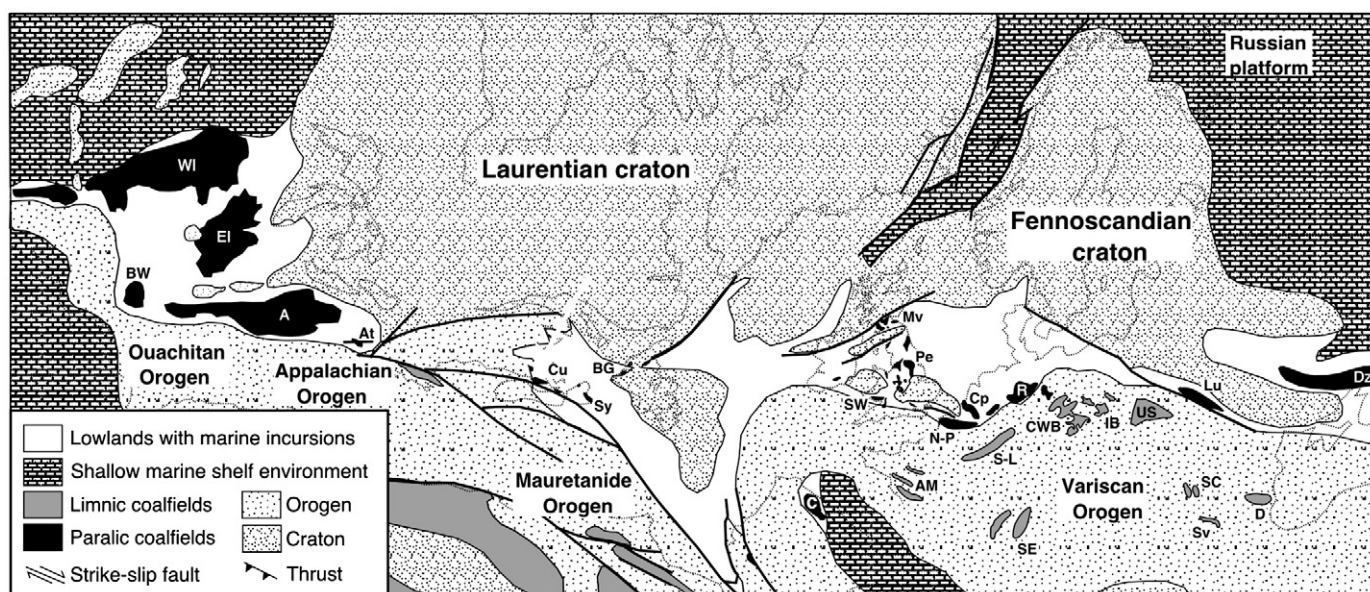


Fig. 3. Pennsylvanian tropical basins. Key from west to east, Western Interior (WI), Eastern Interior (EI), Appalachian (A), Black Warrior (BW), Anthracite (At), Cumberland (Cu), Sydney (Sy), Bay St. George (BG), South Wales (SW), Midland Valley (Mv), Pennine (Pe), Campine (Cp), Ruhr (R), Pas-de-Calais, Nord, Namur (N-P), Armorican (AM), Saar-Lorraine (S-L), Saint Etienne (SE), Central and Western Bohemia (CWB), Intrasedimentary Basin (IS), Upper Silesia (US), South Carpathians (SC), Svoje (Sv), Dobrudzha (D), Lublin (Lu), and Donetz (Dz).

Falcon-Lang et al., 2006.

elevational differences. It also may have occurred in some intermontane limnic basins of the Late Pennsylvanian in Europe (Falcon-Lang, 2004b).

Because wetland floras are so well known, the objective of this paper is to examine the evidence of lowland basinal floras from seasonally-dry environments. Seasonally-dry vegetation probably was as representative of the Pennsylvanian tropical lowlands as that of peat-forming wetlands. Together these two floras are part of the record of oscillating climatic conditions. The discussions presented herein are restricted to areas of low relief, low elevation, and low surficial gradients within the confines of Pennsylvanian sedimentary basins. No attempt is made to evaluate vegetation or climate controlled by areas of high relief, high elevation, mountainous terrains, or extratropical latitudes.

2. Preservation biases in the Pennsylvanian equatorial lowlands

Evidence of plants from the tropical regions of the Pennsylvanian Subperiod is systematically biased in several ways, some common to the deep fossil record of all organic remains in terrestrial environments and some unique to accumulations of plant remains.

The most significant of these systematic biases is the restriction of fossil-plant-bearing deposits almost entirely to basinal lowlands. Basins were regions where long-term accommodation space for sediment burial occurred. Not all such basins were open to the sea, such as the Variscan orogenic basins of central Europe (e.g., Opluštil and Cleal, 2007), but they were nonetheless of low enough elevation during aggradation, probably near sea level, to avoid subsequent erosional obliteration.

Erosion has removed virtually all those Pennsylvanian-age deposits that formed well above sea level in true upland, extrabasinal areas. Thus, it is simply incorrect to refer to an autochthonous or parautochthonous macrofossil plant deposit as “upland” or “extrabasinal.” If it is found in the fossil record, it is preserved in a basinal lowland. This does not mean there were no plants growing in extrabasinal areas, or that elements of such floras could not have been transported into basins, and preserved as exotics. Such truly allochthonous, extrabasinal elements can be detected under certain circumstances where the sedimentary environment is well understood (Greenwood, 1991). In order to conclude, however, that a megafossil was transported into a basinal deposit from a seasonally-dry upland area, an inferential leap and/or independent evidence are needed, in addition to the morphology of the plant itself, to tie the plant to an upland seasonally-dry habitat (Hill, 1981). Generally, allochthonous elements are tough plant parts of species with strong construction, given that only erosion-resistant, structurally competent remains can survive transport over long distances, especially if they come into contact with fluvial bed loads (see Behrensmeyer and Hook, 1992; Behrensmeyer et al., 2000; Ferguson, 2005). When found, such elements are usually of a fragmentary nature and most often are found in areas proximate to known tectonically active, elevated areas (Lyons and Darrah, 1989; Galtier et al., 1992; Falcon-Lang and Bashforth, 2004; Gastaldo and Degges, 2007). Elements of pollen-spore floras, such as bisaccate-striate pollen known to be produced by conifers, are perhaps the most likely allochthonous extrabasinal elements to be preserved within basinal regions (e.g., Zhou, 1994; Peppers, 1997; Falcon-Lang, 2004a; Dimitrova and Cleal, 2007), and may have been carried in by water or by wind (Farley, 1988).

Another taphonomic megabias (*sensu* Behrensmeyer et al., 2000) characteristic of the plant fossil record is the vast over-representation of plants growing in or around wet habitats (Spicer, 1981; Scheiing and Pfefferkorn, 1984; Burnham, 1989), which may be non-representative of the broader landscape, especially if regional climate was seasonally dry. Most plant deposits are parautochthonous (*sensu* Bateman, 1991: plant remains deposited in the same environment in which the parent plants grew, with little transport) or autochtho-

nous (preserved in place). Plant leaf remains and most reproductive organs are fragile and, thus, are most likely to be deposited near the parent plants (Burnham, 1989, 1993). They will usually be rapidly ground into highly particulate debris if brought into contact with sediment in moving water. Furthermore, buried plant leaves and most reproductive organs are difficult to rework without fragmentation and destruction (Gastaldo et al., 1996). Wood and pollen-spores are the most likely to persist and often reveal their history of transport through damage or rounding (Gastaldo et al., 1987, 1993), although well-preserved allochthonous plant parts, including leaves, can be found in some sedimentary environments, especially if transported in the water column by major rivers (Gastaldo et al., 1987). Thus, most macro-plant remains are likely to be found in bodies of standing or sluggishly moving water such as swamps, lakes and ponds, or in nearly abandoned channels (Greenwood, 1991). Plants can be found in bars of active channels, in which deposition of plant remains occurs in slack water phases or where plant parts are deposited in the base of troughs as lags during or in the waning phases of active sediment transport associated with floods (Gastaldo and Huc, 1992). Peat also is an atypical deposit, formed in place under humid to perhumid climatic conditions and not as a result of the kinds of particulate transport characteristic of clastic sedimentation; allochthonous peats have been identified in some modern environments (Gastaldo et al., 1987, 1993) but appear to be non-analogues for economic coal beds of the Pennsylvanian geological record.

In most cases, therefore, the source plants of autochthonous and parautochthonous floras grew immediately adjacent to, or quite near, wet or standing-water habitats, often at the margins of the habitats where preservation occurred (Scheiing and Pfefferkorn, 1984). In such cases, the plants will reflect most closely the conditions immediately adjacent to the area in which they were preserved. Fortunately, though, at a larger scale, the species pool of a region will tend to reflect prevailing climate. Consequently, during periods of seasonally-dry-to-arid climate, the plants growing around the margins of water bodies will likely reflect the overall landscape moisture deficit, unless they were growing directly in standing water or in high soil moisture environments such as swamps, which are often compositionally distinct from the *terra firma* environments that immediately surround them (Knoll, 1985; summary in DiMichele et al., 2001).

3. Climatic framework and drivers during the Pennsylvanian

The extent of glaciation during the later Middle and Late Pennsylvanian is uncertain. The Pennsylvanian has long been considered a time period of extensive, grounded, continental, ice sheets in the south polar regions (e.g., Frakes et al., 1992). More recent work (e.g., Isbell et al., 2003a,b; Fielding et al., 2008) suggests that intervals of time between several discrete, short-lived (1-to-7 myr) glaciations were characterized by greatly diminished ice volume. One of these intervals begins during the late Middle Pennsylvanian (Asturian–early Cantabrian/late Moscovian), when ice volume may have begun to decrease, and culminates in the Late Pennsylvanian (Stephanian/Kasimovian–Gzhelian), when ice volume was significantly reduced. The presence of highly weathered basement surfaces in regions of southern Gondwana (Isbell et al., 2008a,b) suggests that any existing ice during this time was confined to alpine glaciers. The existence of cyclothems throughout the Pennsylvanian and Early Permian (e.g., Weller, 1931; Wanless and Shepard, 1936; Langenheim and Nelson, 1992) has been argued as evidence of persistent high-magnitude (100+ m), high-frequency (10⁴ to 10⁵ kyr) glacioeustatic sea-level changes, corresponding to the Late Paleozoic Ice Age (Heckel, 1986; Heckel et al., 1998; Soreghan and Giles, 1999; Haq and Schutter, 2008). Several recent studies of carbonate and clastic paleotropical successions (Feldman et al., 2005; Bishop et al., 2009), however, document intervals of significantly lower magnitude (2 to

20 m) sea-level changes, in particular, for the late Pennsylvanian (Heckel, 2008; Rygel et al., 2008; Bishop et al., 2010).

It appears that Pennsylvanian ice volume fluctuated regularly on several time scales, as with the Pleistocene and Recent ice age. However, there is also strong evidence for long intervals of significant global warming between intervals of major ice formation, during which time ice volume waned (or diminished) significantly (Isbell et al., 2003b; Fielding et al., 2008). However, there continued to be cyclical variations in sea level and climate in tropical regions.

Variations in sea level are closely linked to variations in climate (Cecil et al., 1985; Cecil, 1990; Cecil et al., 2003a; Olszewski and Patzkowsky, 2003). Such linkages are not merely along narrow coastal belts but appear to be linked to drivers that caused widespread climatic changes across the Euramerican Pangaeon tropics (Cecil et al., 2003a; Poulsen et al., 2007; Peyser and Poulsen, 2008). Furthermore, these climatic changes are yet further linked to patterns of sediment transport. Little transport occurred during times of high, year-round rainfall (humid or perhumid conditions), where sediments were heavily bound by plant rooting, or during times of very low rainfall (arid conditions), where there was insufficient moisture to move sediment long distances. Movement of large amounts of sediment occurred mainly during a wide range of climates with rainfall seasonality, from semi-arid to subhumid. These conclusions are based on empirical studies of modern systems (Schumm, 1968; Cecil, 1990; Cecil et al., 1993; Cecil and Dulong, 2003; Cecil et al., 2003b).

Clothoems thus are records of a spectrum of terrestrial climates. The various rock units record a range of climates varying from those with strongly seasonal rainfall to those where rainfall exceeded evapotranspiration for most of the year. Terrestrial rocks representing the drier end of this spectrum include vertic paleosols, often calcic. Studies of modern vertic soils (Nordt et al., 2006) indicate that carbonate will begin to form at relatively high mean annual rainfall amounts near 1400 mm, seasonality being key (mainly semi-arid to subhumid climates). On the wet end of terrestrial rocks are paleosols such as paleo-Spodosols, Ultisols, and Oxisols, recording humid to perhumid conditions (Cecil et al., 2003a). Coal beds, derived from peats, further reflect not only high mean annual rainfall, but a distribution of precipitation such that it exceeds evapotranspiration for between 10 and 12 months a year (humid to perhumid climates), suppressing the oxidation of surface organic accumulations and contributing to their burial (Cecil, 1990).

Global Climate Simulation (GCS) models of Pennsylvanian–Permian climate (Poulsen et al., 2007; Peyser and Poulsen, 2008) in general are consistent with these climatic interpretations based upon the rock record (Cecil, 1990; Cecil et al., 2003a; Driese and Ober, 2005). These GCS models suggest seasonality of rainfall in low latitudes, particularly at glacial minimum and high rainfall close to glacial maximum, a pattern inferred to result from the strengthening of Hadley Cell circulation patterns along the Intertropical Convergence Zone (ITCZ).

A subtext of this climate discourse relates to the behavior of sea level relative to basinal geometry and climate. Basins in the west-central to western parts of the Pangaeon equatorial zone, the Illinois Basin and Western Interior regions, and the Appalachian foreland basin, which was connected to mid-continent cratonic regions, were extremely flat during the later Middle and Late Pennsylvanian. Topographically irregular following the mid-Carboniferous lowstand and attendant unconformity (Siever, 1951; Blake and Beuthin, 2008), these vast American basins gradually filled again during a long-term rise in average global sea level (Haq and Schutter, 2008; Rygel et al., 2008). Consequently, by the later Middle Pennsylvanian, small changes in global sea level could have had profound effects on the extent of the sea covering the continental interiors, with both rapid inundation during sea-level rise and rapid exposure of the land surface during sea-level fall (Cecil et al., 2003a). The presence of

Vertisols, (sometimes with remnant calcic features) beneath coal beds records exposure of continental areas to long periods of climate seasonality prior to the progressive development of seasonally wet climates. A further consequence of the flat landscapes of the late Middle and Late Pennsylvanian are widespread coal beds, which extensive outcrop and subsurface mapping show to extend and be continuous over entire basins and even among basins (Cecil et al., 2003a; Greb et al., 2003), reflecting the widespread effects of regional climatic conditions. These coals do not appear to have formed in narrow time-transgressive, coastal belts.

In contrast to the large cratonic basins of North America and the Appalachian foreland basin, there also were many smaller basins that formed in association with the Variscan orogeny, which began in the Late Devonian and continued into the Early Permian in some areas (Leveridge and Hartley, 2006; McCann et al., 2006). Many of these basins are part of the Variscan Foreland Complex, which stretched from eastern Europe through eastern North America (Rast, 1984; Calder, 1998; Falcon-Lang et al., 2004, 2006; Opluštil and Cleal, 2007). In a number of these basins, marine influence is extremely limited, and the locus of peat formation appears to have shifted from coastal paralic to more inland, intramontane positions. Upland areas were much more proximate to many of these small basins than in the large, flat basins of the west-central and western Pangaeon craton. This should have increased the likelihood of finding allochthonous extrabasinal elements within such basins during times of climatically wetter periods of peat formation, which is indeed the case (Lyons and Darrah, 1989; Libertín et al., 2009). However, the same cycles of linked sea level and climate that affected the cratonic basins from the Appalachians through Mid-continent North America also should have had some effect on patterns in these smaller basins, even if they were disconnected from direct effects of sea-level change. In some of these basins, the basal fill is paralic and upper fill entirely non-marine (e.g., Czech Republic/Poland) and lithological cycles, probably linked to climate, occur throughout (Havlena, 1961; Gastaldo, 1996; Falcon-Lang, 2003a; Opluštil and Cleal, 2007). These intramontane basins may actually be more likely to preserve the “inter-coal-bed” floras more faithfully than the large paralic basins because marine waters did not invade them during the periods between peat formation to the same extent. Instead, clastic terrestrial rock sequences are more common (Gastaldo, 1996; Opluštil and Pešek, 1998; Falcon-Lang, 2003b; Falcon-Lang and Bashforth, 2004; Falcon-Lang, 2006; Opluštil et al., 2009). However, during the times of peat formation, the slopes of the basinal areas probably were not populated by dryland vegetation (e.g., Opluštil et al., 2007, 2009). For a modern analogue, consider the mountainous regions of northern Sumatra where rainfall exceeds evapotranspiration for 11–12 months a year. Dense rain forest covers the steep slopes and the streams are black-water, carrying extremely limited amounts of suspended and dissolved sediments, except for organics (Cecil et al., 2003b).

The vertically stratified vegetational zones inferred for the small, intermontane basins (e.g., Libertín et al., 2009) may have been mimicked over much larger spatial scales in the flatter cratonic areas. Cecil et al. (2003a), for example, have shown a low stand, paleo-latitudinal, precipitation gradient from humid conditions in west-central Pangaea (Appalachian basin) to moist subhumid farther to the west, to semi-arid in western Pangaea. Given the known linkages of vegetation and climate, it is to be expected that the vegetation of these areas with different rainfall regimes would have differed also.

4. What grew in the lowland basins when they were climatically dry?

Vegetation and its plant species composition closely reflect climate today (Claussen, 1998). Consequently, it has been possible to develop both static and dynamic schemes for describing the distribution of modern global vegetation (e.g., Holdridge, 1967; Walter, 1985;

Woodward et al., 2004). There is every reason to believe that plants of the past, including the Paleozoic, would have had similar ties and responses to climate as the primary control on their biogeographic distributions (Wolfe, 1978; Phillips and Peppers, 1984; Falcon-Lang, 2004a; Montañez et al., 2007). Schemes describing late Paleozoic plant biogeography (e.g., Ziegler, 1990; Rees et al., 2002) have been built on this assumption, which is consistent with empirical data.

The picture of late Paleozoic vegetational dynamics within the equatorial tropical region is, however, incomplete. Those floras that occupied basinal lowlands during times of seasonal dryness are not nearly as well known as those of the wetlands, and there are few extensively studied examples. To say that floras of subhumid to semi-arid climates are poorly known, though, would be an overstatement, given that a few are quite well characterized. Those few, however, are of two broad types. One appears to be transitional between wetland and more seasonally-dry floras, such as some of those described from Nova Scotia (Falcon-Lang, 2003a,b, 2004a; Falcon-Lang et al., 2004; Falcon-Lang, 2006), and probably grew under humid to variably seasonal climates. Such floras are typified by a subset of the same clades that dominated the wetlands (dominantly medullosan pteridosperms and cordaitaleans), but in different proportions and often comprising different species. The second type consists of floras that differ significantly in composition from those of the wetlands, dominated by and/or containing a large proportion of different genera, families and even orders, in other words, containing many different evolutionary lineages. These floras are known primarily from intensively studied small deposits, often single outcrops preserving limited channel-fill or small lake deposits. Allochthonous palynological and macrofossil remains have led to the inference that these exotic floras always lived in seasonally moisture stressed areas outside of the basins. Their habitats are envisioned as “well drained,” or perhaps located in seasonally-dry extratropical or paratropical (*sensu* Wolfe, 1978) areas, during the times when humid-perhumid climates typified tropical “wet” lowlands. The dynamic distribution on the landscape of these more xeric floral types, however, is not well known empirically. Much can be inferred based on the patterns of preservation, such as the presence of allochthonous remains preserved in deposits proximate to contemporaneous rising upland areas (Chaloner, 1958; Lyons and Darrah, 1989) that indicate much wider distributions than just “uplands” or “extrabasinal,” including periods of occupation of the basins themselves.

4.1. Paleosol indicators of seasonal climates

Paleosols are possibly the most powerful indicators of the degree of climatic seasonality in the paleotropics, as well as the effects of that seasonality on plants and vegetation. A wide spectrum of paleosol Orders is known from Pennsylvanian-age equatorial regions.

At the wettest end are organic Histosols – the peat bodies themselves, diagenetically modified into coal beds. The internal structure of coal beds revealed by petrographic studies, and the study of coal balls and palynology reveal considerable dynamism in these deposits, including periods of peat decay, flooding, and fire, punctuated by intervals of rapid peat formation (e.g.: Phillips et al., 1985; Bartram, 1987; Eble and Grady, 1990; Peppers, 1996; Hower and Eble, 2004).

Beneath a coal-bed Histosol there generally is a so-called underclay or seat-earth, which itself is a paleosol that developed prior to peat formation. Most are ancient mineral soils formed under variable degrees of seasonality of rainfall. Throughout the Middle Pennsylvanian, seat-earth paleosols are Spodosols, Ultisols, ferric Vertisols and Argillisols, some of the latter with calcic nodules. In the modern world such soils form under well-drained conditions and relatively high soil moisture regimes (Cecil and Dulong, 2003; Cecil et al., 2003a; Driese and Ober, 2005; Nordt et al., 2006). Later Middle Pennsylvanian seat-earth paleosols in the United States often have vertic features

indicative of strong seasonality of rainfall (Cecil et al., 2003a; Falcon-Lang, 2004a) (Fig. 4A). Red Vertisols and calcic Vertisols (Fig. 4B) are much more common in the Late Pennsylvanian throughout the Pennsylvanian coal belt of the U.S. (Joeckel, 1989, 1994, 1995; Feldman et al., 2005), and can be the lateral equivalents of lacustrine carbonates in the Appalachian basin.

Most seat-earth paleosols, which formed for some-to-most of their development under varying degrees of rainfall seasonality, appear to have been subject to progressive increase in the number of wet months, before the onset of peat formation. These mineral soils generally are gleyed often very deeply to entirely, something superimposed on the pre-existing soil profile (Fig. 4). This gleying indicates a progression from the seasonally-dry conditions, under which the soil first began to form, to the development of humid conditions, with moisture becoming more continuously distributed, along with rising water tables sometime prior to the onset of peat formation. The contact between the coal bed and seat-earth paleosol can vary from gradational to paraconformable to disconformable. Where the complete underclay soil profile is present, as is commonly the case, paraconformable contacts suggest continuation of increasing rainfall, rising water table and perpetual drowning of the mineral surface, leading to the onset of peat formation. Gradational contacts may reflect a mineral swamp deposit between the top of the seat-earth paleosol and the base of the coal bed. The position of paleosols



Fig. 4. Pennsylvanian paleosols. A. Danville (no. 7) Coal (Histosol) and (vertic) seat-earth paleosol (blocky, slickensided, rooted olive siltstone), late Middle Pennsylvanian, Indiana. Seat-earth paleosol is fully gleyed. B. Cohn Coal (Histosol) overlying a thick seat-earth paleosol (calcic Vertisol), Upper Pennsylvanian (Missourian), Illinois. Soil profile is fully gleyed.

immediately beneath coal beds and the presence of gleying indicate strong climatic contrasts, with a late stage transitional climate, getting wetter (Driese and Ober, 2005), finally leading to peraquic soil conditions, and the development of Histosols (Table 1). The couplets of mineral paleosol and Histosol suggest a progressive increase in rainfall accompanied by diminishing seasonality. The different climate signals no doubt were accompanied by strong vegetational contrasts.

Temporal and spatial climate gradients within and among Middle Pennsylvanian cyclothems have been documented along both longitudinal gradients, from the low latitudes of west-central Pangaea (eastern USA) to western Pangaea (western USA), and on latitudinal gradients, northward from the edge of the tropical zone (Cecil, 1990; Cecil et al., 2003a; Poulsen et al., 2007). These studies indicate patterns of east-to-west and north-south climatic drying. Both the temporal and spatial trends in precipitation suggest that the region was in a belt of prevailing easterly winds with an east-to-west progression in rainout. In particular, west-central Pangaea was more humid than western Pangaea during the Pennsylvanian (Cecil et al., 2003a). The coal beds in east-central Pangaea (western Europe) through to the Tethyan border regions, suggest that the latitudinal climate gradient was at a continental scale.

The overall paleoclimate profile of the Late Pennsylvanian appears to have been shifted to the drier end of the spectrum, perhaps with an increase in the magnitude and duration of seasonality at the drier end (White, 1913a; Cecil et al., 1985; Phillips et al., 1985; Cecil, 1990; Olszewski and Patzkowsky, 2003; Feldman et al., 2005; Bishop et al., 2010; Gulbranson et al., in press). In the early parts of the Late Pennsylvanian (Missourian), seat-earth paleosols often have well developed vertic features and commonly may contain calcic horizons. Such features indicate formation under climates with seasonal moisture deficits, in some cases with evapotranspiration exceeding rainfall for many months of the year, and rainfall less than 1400 mm/year (Nordt et al., 2006) (Table 1).

The morphology of roots preserved within soil profiles allows some inferences about the parent vegetation. Because many soils have complex histories of formation, however, the roots preserved in the uppermost parts of a profile may not reflect the plants that grew on the soil for most of its existence. So, for example, stigmairian root systems of lycopsid trees likely represent late stage vegetation in the transition from well-drained mineral soils to peat formation. The same is true for the fine root masses, likely derived from pteridosperms and calamitaleans, often found in weakly laminated sediments rich in plant fossils, which sometimes occur between the underlying mineral paleosol and base of the coal, indicative of surficial standing water. On the other hand, roots diagnostic of non-wetland plants may occur, often encrusted with calcium carbonate (Fig. 5C), especially in paleosols that do not underlie coal beds or indicate terminal transitioning to humid-perhumid climates. There also are abundant

paleosols, particularly in the Late Pennsylvanian, that occur between coal beds, but not in a seat-earth stratigraphic position. For the most part, these paleosols do not preserve macrofossils or pollen and spores, so the flora can be inferred only generally by analogy to the vegetation of modern soils (Table 1).

An example of a paleosol with unusual roots preserved within it comes from the early Late Pennsylvanian (Missourian) portion of the Conemaugh Formation of West Virginia (Fig. 5A). The soil is from the “Pittsburgh reds” interval and has vertic features, including calcium carbonate nodules and carbonate encrustations around the roots. The paleosol in question contains downwardly forking root casts encased in carbonate (Fig. 5B–C). The roots are found between 2 and 4 m below the upper surface of the paleosol, indicating deep penetration into the substrate. These roots provide some, albeit limited, insight into the flora that grew on the soil surface. Certain plant groups can be eliminated immediately as the source of the roots. These include marattialeans tree ferns, calamitean sphenopsids, medullosan pteridospermous seed plants, and lycopsids. None of these plants are known to have had root systems this deeply penetrating. The marattialeans had adventitious root systems that mantled the trunk and spread out shallowly around the tree after reaching the soil surface (Ehret and Phillips, 1977). Because they were capable of recovering from burial to a certain extent, such root systems enabled these plants to live in wet to periodically flooded soils with moderate sediment accumulation rates (Falcon-Lang, 2003c). Medullosan pteridosperms had a variety of fibrous roots (Rothwell and Whiteside, 1974), some of which may have acted as prop roots, forming a small root mantle that appears to have penetrated moist soils only shallowly. Calamitean roots were similar to those of pteridosperms in being fibrous and shallowly penetrating (Dawson, 1851). Finally, lycopsids had stigmairian root systems that were shallowly penetrating and spread widely around the tree (Frankenburg and Eggert, 1969), although there have been suggestions of somewhat deeper penetration of soils by sigillarian root systems than by those of other lycopsids (Eggert, 1972; Pfefferkorn and Wang, 2009).

There remain a large number of other possible plants as the source of the above-mentioned deep, straight roots. However, these are all plants inferred from other botanical and geological sources to have lived under conditions of seasonal moisture deficits. The two most likely suspects for the origin of these roots are conifers and cordaitaleans. Both are reported from basinal lowland deposits of this age, so access to the area is assured. Both have been determined to be large woody trees, and cordaitalean roots have been well characterized as of a robust, woody character (Cridland, 1964; Falcon-Lang and Bashforth, 2004). In neither of these groups, however, have there been confirmed reports of deeply penetrating roots, as opposed to the shallow root-plates typical of most trees in seasonal habitats, though Falcon-Lang and Bashforth (2005) have

Table 1

The basin geometry for the genesis of soils and their characteristics presented herein is one of very low relief and very low surficial gradient, as in the basin floor of the modern Gulf of Carpentaria, Australia (~1 ft/mile) (Edgar et al., 2003). Soil moisture regimes are adapted from the US Department of Agriculture Keys to Soil Taxonomy as are the soil orders (Soil Survey Staff, 1999). Paleosol nutrient status and/or cation concentration interpretations are based on known characteristics of modern soil orders. Climate interpretations are based on the climate classification of Cecil, 2003 and, Cecil and Dulong, 2003.

Soil moisture classification	Soil moisture condition	Soil order	Nutrient status or cation concentration	Climate	Probable flora
Peraquic	Constantly water logged	Histosols	Oligotrophic	Perhumid to humid	Low diversity, specialist flora, nutrient stress
Aquic	Water logged most of the time	Histosols	Oligotrophic	Humid	Higher diversity, specialist flora, nutrient stress
Perudic	Moist throughout the year	Oxisols, Ultisols Spodosols	Oligotrophic	Humid to moist subhumid	Luxuriant
Udic	Moist, dry no more than 90 days	Vertisols	Mesotrophic to eutrophic, noncalcic	Moist subhumid	Luxuriant to mesophytic
Ustic	Intermediate between udic and aridic	Vertisol	Eutrophic, calcic	Dry subhumid	Mesophytic
Aridic and torric	Dry and hot, never moist for more than 90 days throughout the year	Aridisols	Natric (enriched in alkaline and alkaline earth cations)	Semi-arid to arid	Xerophytic

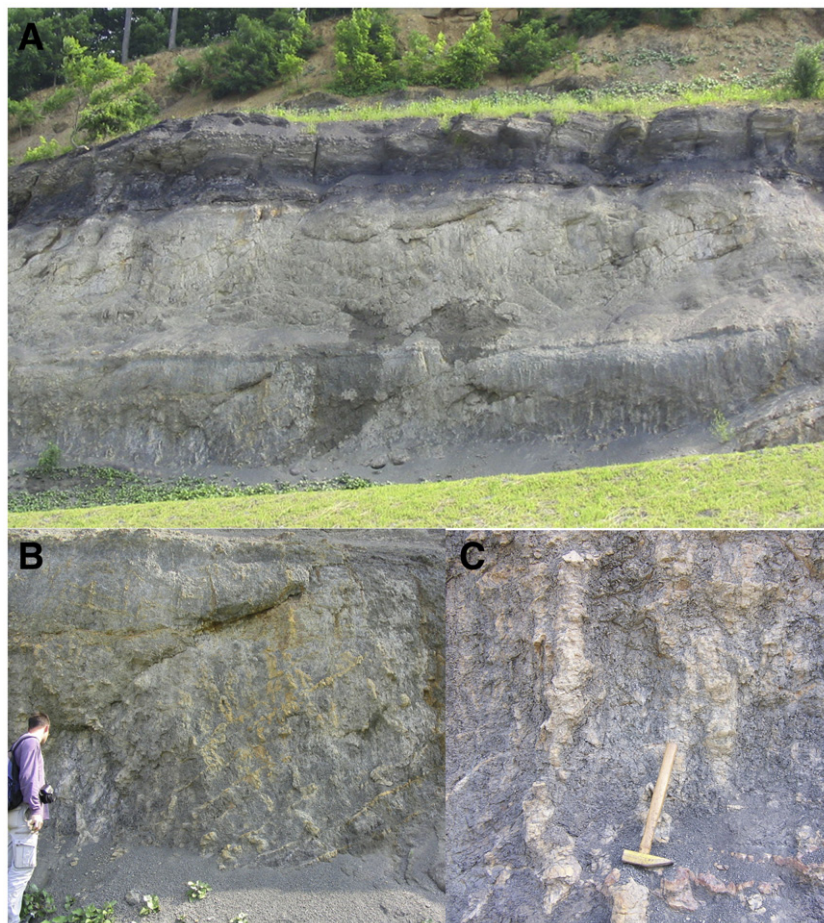


Fig. 5. Paleosol near Goshen Road Exit, US Interstate Highway 79, West Virginia. A. Compound calcic Vertisol with vertically disposed roots in the lower paleosol horizon. B. Lower paleosol horizon showing angular displacement surfaces within which carbonate has been deposited and vertically disposed root casts, encased in carbonate. C. Vertically disposed roots in the lower paleosol horizon.

reported vertical taproots extending from the base of a cordaitalean stump. It also is possible that the parent plants might have been peltasperous seed plants, such as callipterids. *Autunia* (*Callipteris conferta*) has been reported in the Appalachians from the Conemaugh Formation (Remy, 1975). However, the habit of this plant is not well understood, even though a shrub to tree form appears likely. Completely unknown plants cannot be ruled out, of course.

4.2. Fossil evidence of seasonally-dry floras

The search for terrestrial floras living in basinal lowlands during “inter-coal” interludes begins with floras that appear to have lived proximate to, but not in, wetland habitats, detectable as allochthonous debris transported into basins from surrounding “uplands.” Such floras were described as “Flözfern” assemblages by Havlena (e.g., Havlena, 1961; see also Gastaldo, 1996, for an English summary of Havlena’s work). Flözfern floras were contrasted with “Flöznah” floras, those considered to have contributed to peat formation or to have grown in wetlands intimately associated with peat formation. Elevation rather than climate was originally considered as the primary cause of differences between the hygromorphic floras associated with coals and the more meso-to-xeromorphic plants characteristic of the Flözfern assemblages. Havlena (1971) eventually subdivided the Flözfern floras into a nearer and further assemblage, both seed-plant dominated, the latter often containing conifers in the later Pennsylvanian. Gastaldo (1996) modified this concept to place it within a climatic context, noting that the Flözfern and Flöznah assemblages probably represent different biomes under different climatic condi-

tions. The presence of the former in the basins between coal beds more likely represents climate change, in this latter scenario, than simply transport of exotic elements into the basinal lowlands by mechanical means under otherwise stationary climatic conditions.

Plants preserved in marine rocks also provide a means to assess vegetation living between times of peat formation. One of the earliest conceptualizations of the potential in this kind of deposit is the “Neves effect” of Chaloner (1958), where pollen from cordaitaleans found in marine rocks was thought to have been derived from upland habitats, brought closer to marine conditions by sea-level rise. This model does not account, however, for the covariance between sea-level rise and regional to global climatic changes. Marine rocks may have formed at times when climate was trending toward more seasonality of rainfall than during the humid to perhumid periods of peat development. Stopes and Watson (1909) and, more recently, Scott et al. (1997) described plants of Early Pennsylvanian (Langsettian) age in marine nodules that included goniatites and plants. The plants in these marine deposits belong to genera and families that, at the time, appear to have grown in clastic wetlands but not in contemporaneous peat-forming habitats, based on coal-ball floras. The nodule floras, dominated by medullosan pteridosperms and ferns, include such things as the medullosans *Sutcliffia*, *Poroxydon*, and *Cycadoxylon*, and the ferns *Tubicaulis* and *Zygopteris*. Mapes and colleagues have described small petrified plants from Late Pennsylvanian marine black shales (Rice et al., 1996; Rothwell et al., 1996; Mapes and Mapes, 1997; Rothwell et al., 1997; Dunn et al., 2002) that are distinct from those found in wetland assemblages, including some similar elements, but many that are entirely distinct. These floras suggest that

the plants living in the basinal lowlands during the times of marine shale deposition were growing under different physical conditions than the wetland floras, and probably under slightly-to-moderately different climatic conditions (given the close association between floristic composition and climate).

4.2.1. Cordaitalean-rich floras

The cordaitaleans, close relatives of the conifers (Hilton and Bateman, 2006), encompass many species, growth morphologies, and habitat preferences, a realization that has come from paleoecological studies supported by detailed analysis of leaf characteristics suggesting considerable taxonomic diversity within the group (e.g., Šimůnek, 2007, 2008). Preferred habitats range from peat-forming and clastic wetlands, through increasingly seasonally-dry settings, into some of the most well-drained and drought-prone habitats of the Pennsylvanian tropical realm (Falcon-Lang and Bashforth, 2005). Cordaitalean branches in dryland settings have weak growth rings (Falcon-Lang, 2007) though no rings in mature wood, characteristic of growth under weak climatic seasonality. Branches are most exposed and susceptible to environmental fluctuations.

For many years cordaitaleans were conceived as strictly “upland” plants, despite frequent occurrences in basinal lowland deposits. In this case, the term “upland” really was being used as shorthand for relatively dry habitats. Chaloner (1958) coined the term “Neves effect” to explain the occurrence of cordaitalean pollen in marine sediments, suggesting that rising sea level brought plants of higher elevation, better-drained areas into proximity of marine environments during transgressions (Falcon-Lang, 2004b). A different interpretation of this observation links it to climate change and ensuing vegetational change. The appearance of “upland” cordaitaleans may represent a transition from coastal wetlands to circum-coastal, seasonally-dry habitats. As a result, a different kind of cordaitalean would be represented by pollen in the post-coal marine rocks than those represented by pollen and macrofossils in coals and other coastal wetland settings.

More recent evidence has established unequivocally that cordaitaleans were important to dominant elements in humid and perhaps perhumid peat-forming environments, especially during the later Early and early Middle Pennsylvanian (late Duckmantian to early Bolsovian) (Phillips and Peppers, 1984), but continuing throughout the entire period of peat-swamp development in the Euramerican tropical realm (Costanza, 1985; Trivett and Rothwell, 1991). Cridland (1964) suggested, based principally on gross morphology, that these lowland, wetland cordaitaleans might have been mangroves, a determination that has been controversial (Raymond and Phillips, 1983; Raymond, 1987, 1988). Though a mangrove habit seems possible, the interpretation remains in doubt (Raymond et al., 2001; Falcon-Lang, 2005), including the degree of salinity that cordaitaleans could tolerate (Falcon-Lang and Miller, 2007).

The growth of cordaitaleans in environments with periodic moisture deficits does, however, appear to be the center of both biodiversity and ecological dominance of the group. Some of these plants were centered in areas that were transitional between strongly seasonally-dry and humid lowland settings, particularly in better-drained floodplains subject to wildfires (Falcon-Lang, 2003b,c; Falcon-Lang et al., 2004; DiMichele et al., 2005; Šimůnek, 2008). In these settings, the cordaitaleans are associated with pteridosperms, minor amounts of calamitaleans, and even sigillarian lycopsids, which may have been growing around persistent wet areas on the landscape (Falcon-Lang et al., 2004).

At their environmental extreme, cordaitaleans appear to have been among the dominant forest trees in areas subject to strong seasonal drought. Based on Early and Middle Pennsylvanian-age log jams of transported cordaitalean stems, it has been speculated that they forested slopes adjoining basinal areas (early literature summarized in Falcon-Lang and Bashforth, 2004, 2005; Gastaldo and Degges,

2007). However, these plants also have been documented in basinal lowlands, where well-preserved, parautochthonous to autochthonous stands have been found, with tree heights estimated to have been nearly 50 m (Falcon-Lang, 2003c; Falcon-Lang and Bashforth, 2005). In addition, they have been documented as dominant elements of parautochthonous floras in incised valley deposits laterally equivalent to Vertisols and calcic Vertisols (Feldman et al., 2005; Falcon-Lang et al., 2009), of Middle and Late Pennsylvanian age. This has been observed in the mid-continent Illinois and Western Interior basins, long distances from contemporaneous upland areas, with low regional geographic gradients. The plant remains occur in intra-formational channel fill, precluding long-distance transport and strongly suggestive of limited moisture on the landscape (Feldman et al., 2005; personal observations of the authors, 2008 and 2009). In these latter instances, cordaitaleans are occasionally found in association with conifer remains.

4.2.2. *Megalopteris* and *Lesleya* floras

Floras containing various combinations of *Megalopteris*, *Lesleya* and other xeromorphic plants are among the earliest known Pennsylvanian-age parautochthonous, non-wetland floras. They occur in basinal clastic sediments deposited between intervals of peat formation. These floras are reported from the Illinois Basin (e.g., Canright, 1959), Michigan Basin (Arnold, 1934, 1949), and Ohio in the Appalachian Basin (Andrews, 1875; Cross, 1962), and continental Europe (Remy and Remy, 1975; Šimůnek, 1996). Although the flora is known from the Early Pennsylvanian, all those occurrences in coal basins are of Middle Pennsylvanian age. Where it can be determined from descriptions in the literature or from collections made by the authors, all occurrences but one are from clastic rocks in depositional settings not associated with the coal beds (that is, not in the coals, nor in partings within the coals, nor in the immediate roof rocks, in those settings where the roof floras represent the final phases of the peat swamp or early siliciclastic deposition within wet floodbasins — see Gastaldo et al., 1995). The exception to this rule is a report from the high-ash Lubná Coal in the Czech Republic (Šimůnek, 1996; Opluštil et al., 2007).

Compositionally the diagnostic elements of these floras are the foliage types *Megalopteris* and *Lesleya*, thought to be seed plants (Leary and Pfefferkorn, 1977; Leary, 1990). From published illustrations, some of the plants initially identified as *Megalopteris* appear, in fact, to be *Lesleya*, based on leaf-venation patterns. The floras also may contain other seed plants, including leaves attributable to *Cordaites*, which is a very broad group taxonomically, encompassing a wide range of ecological tolerances (see further discussion below).

This kind of vegetation has been described most fully from earliest Pennsylvanian, non-coal-bearing sequences. In these rocks, clastic, plant-bearing sediments are preserved in incised channels within limestone bedrock along the northwestern margin of the Illinois Basin (Leary and Pfefferkorn, 1977; Leary, 1981), and to a lesser degree from a number of other Illinois Basin-margin localities preserved in sinkholes or deeply incised channels in limestone bedrock (e.g., Lesquereux, 1884; White, 1908). The flora also has been reported to occur elsewhere at the same time in entirely clastic intervals, possibly formed under seasonally-dry climates, such as the Fern Ledges locality in the Maritime Provinces (Stopes, 1914; Wagner, 2005; Falcon-Lang, 2006; Falcon-Lang and Miller, 2007) and southern England (Cleal and Thomas, 2004). All of these floras come from the lower part of the Pennsylvanian succession, in some instances immediately above the mid-Carboniferous unconformity surface. There are strong suggestions, given the conditions in which the plants are preserved in both Illinois and the Maritimes, that the flora was a specialist one that favored soils derived from limestone parent material (White, 1908; Remy and Remy, 1975; Leary and Pfefferkorn, 1977). Such soils are often subject to drought and low nutrient conditions, so it is possible that this flora was an edaphic specialist assemblage, which would be

consistent with the morphological features of the dominant plants (e.g. Remy and Remy, 1975, on the morphology of *Lesleya*).

Within coal-bearing sequences, two occurrences of this flora are known from Indiana on the eastern shelf of the Illinois Basin and one from the Czech Republic. The first Illinois Basin occurrence is reported briefly and without details by Canright (1959), from the Brazil Formation of late Atokan age (Peppers, 1997). Though details of the outcrop and sedimentological features of the deposit are not discussed by Canright (1959), the stratigraphic position is approximately the same, and the geographic location near to that of the second collection, which was made by one of the authors of this paper in the 1980s. This second flora is also from the upper Brazil Formation in Indiana. Here the flora occurred in coarse siltstone, with a limestone below, and a sequence of mudstones above, with the Minshall Coal bed at the top of the sequence. The flora consists of mostly complete leaves, densely packed, as if subjected to minimal transport, and is dominated by cordaitalean gymnosperms, with rare *Lesleya* sp. and an unidentified pinnate leaf with parallel veins in the pinnules. Isolated specimens of tree-fern foliage, *Pecopteris* sp., and pteridosperm foliage also occur in the assemblage. The Czech Republic occurrence is from a dark mudstone in the Chotikov group of coal seams, of late Asturian (Desmoinesian) age (Šimůnek, 1996; Opluštil et al., 2007; Šimůnek, 2008). It occurs in association with cordaitaleans, pteridosperms and sphenopsids, elements of typical peat-forming vegetation; however, the flora also includes other less common taxa, such as *Rhacopteris*, *Dicranophyllum*, *Sauropteris*, and *Palaeopteridium*, atypical of wetland floras (Opluštil, personal communication, 2009). There evidently are other, unreported occurrences of *Lesleya* in Czech Carboniferous basins, both in coal-bearing strata and not (Opluštil, personal communication, 2009).

Whereas the earliest Pennsylvanian *Megalopteris* and *Lesleya*-rich floras do not qualify as “intra-coal-bed” basinal floras, they do give us some indication that later floras may have been associated with environments that had periodic soil moisture deficits, possibly on high pH, limestone-derived soils. The Atokan assemblages can be seen as a reappearance after a stratigraphic gap that encompasses most of the Morrowan and Atokan (Langsettian, Duckmantian and most of the Bolsovian). However, given the peculiar preservational circumstances of nearly all examples of this flora, it could be considered fortuitous that we know of it at all. The earliest Pennsylvanian deposits tell us it was “out there” on the landscape probably by some time during the mid-Carboniferous sea-level drawdown. As will be seen with other floras from seasonally-dry settings, early evidence often is scrappy or preserved under unusual circumstances, only to be followed somewhat later by more fully developed floras in the core parts of basinal lowlands. Evidence for the widespread distribution or landscape dominance of this flora, however, remains weak.

The occurrence of this flora in the late Atokan is significant because it was a time interval of global-scale environmental change, manifested in patterns of sedimentation (Bertier et al., 2008), geochemistry (Cecil et al., 1985), and floral composition, even within wetland assemblages (Phillips and Peppers, 1984). Recent studies of glacial records in the southern hemisphere (Fielding et al., 2008), and global sea-level records (Rygel et al., 2008), suggest a significant decline in the mass of grounded ice near Atokan–Desmoinesian boundary time (roughly the Bolsovian–Asturian boundary of the middle Moscovian), which may be the proximate driver of these global changes. Increased periods of seasonal moisture availability, especially combined with limestone substrates, may have favored the reappearance, and occasional establishment, of this flora in basinal lowlands between intervals of peat formation. However, frankly, it is not clear why this particular flora appears at this time, as opposed to the conifer-rich flora, described below, which is floristically distinct. It seems more likely that a conifer-rich flora would have been found. Puzzlement comes from the fact that the conifers were certainly in existence at this time (Scott, 1974) and that earlier conifer

occurrences are known from the Atokan of the Illinois Basin, thus earlier than these *Lesleya* occurrences, but in basin-margin locations (Plotnick et al., 2008, 2009).

4.2.3. Late Mississippian to Late Pennsylvanian floras containing conifers

Primitive conifers are the signature plants of floras from seasonally-dry habitats that differ strongly in composition from humid peat-forming and mineral-soil wetland vegetation (Mapes and Gastaldo, 1986; Broutin et al., 1990; DiMichele and Aronson, 1992; Waters and Davies, 2006). Conifers were not necessarily the dominant elements of these floras, but they did produce foliage-covered branches that were relatively more resistant to transport and decay than were the broad leaves of associated seed plants (Lyons and Darrah, 1989). Consequently, their remains reveal the existence of another type of flora outside of basinal lowlands. Additionally, conifer pollen is distinct, differing considerably from that of humid-climate, wetland plants of the time. This provides another diagnostic means of identifying the proximity of conifer-rich floras to the basins, based on the presence of allochthonous grains in associations otherwise dominated by typical humid-climate taxa (e.g. Zhou, 1994; Rueger, 1996; Eble, 2002; Dimitrova and Cleal, 2007).

4.2.3.1. Latest Mississippian to Middle Pennsylvanian interval. The earliest evidence of putative conifers is palynological. *Potoniesporites*, possible conifer pollen, is common in early Namurian fluvial deposits in Newfoundland (Utting and Giles, 2008) and late Namurian marine bands in the UK suggesting an early origin of conifers just before the Mississippian–Pennsylvanian boundary (Stephenson et al., 2008). Zhou (1994) identified conifer-like pollen grains at paleo-paratropical latitudes in present day China during the Early Pennsylvanian (early Bashkirian). In combination with several other occurrences of similar conifer-like pollen, Zhou (1994) suggested that primitive conifers may have evolved outside the tropics in seasonally xeric settings and moved into the equatorial regions during the Middle Pennsylvanian. The earliest macrofossil identified as a conifer is foliage preserved as charcoal, reported by Scott and Chaloner (1983) from the early Middle Pennsylvanian (Duckmantian) of England. This report has been followed by several reports of younger Middle Pennsylvanian conifer fragments from across the equatorial region, most preserved as allochthonous foliar debris (summarized in Lyons and Darrah, 1989). The earliest stratigraphically well constrained report of conifer remains in North America is from the Middle Pennsylvanian (Atokan) of Colorado (Arnold, 1941). A somewhat less well constrained report is that of Plotnick et al. (2009) from the Illinois Basin, also likely Atokan (Bolsovian).

Most reports of Middle Pennsylvanian conifers appear to have been of allochthonous debris. And, in most instances, the fossils were found only in basins where there were adjacent upland areas from which the conifers could have been transported (Lyons and Darrah, 1989). The allochthonous finds, of course, provide no direct evidence that conifers actually occupied basinal lowlands during the drier parts of climate/sea-level cycles, nor do they rule out this possibility.

There are a few exceptional deposits that demonstrate the unequivocal presence of conifers in basinal lowlands between the intervals of wetlands, peat formation and humid climates. Galtier et al. (1992) report an English occurrence of mid-Middle Pennsylvanian (Bolsovian) age in which a number of small woody stems, 5–15 mm in diameter, were buried in volcanic ash. It was not possible for the authors of this study to determine if the stems were buried in place, however all were vertically disposed. The base of the ash bed rests directly on red–purple mottled paleosols with features indicative of well-drained, oxidizing conditions. Earlier work, e.g., Besly and Turner (1983), suggested that these paleosols were post-depositionally reddened. However, this has since been refuted by later work that characterizes them as having formed under semi-arid conditions (Waters and Davies, 2006). The stems were identified as having

conifer-like wood, as opposed to wood of cordaitalean affinities. The small diameter of these stems supports interpretations by [Hernandez-Castillo et al. \(2001\)](#) that early conifers were relatively small-statured plants. Recently, two finds of conifers in parautochthonous deposits from the Illinois Basin document quite clearly that these plants were actual occupants of the basinal lowlands between times of peat/coal formation, during seasonally-dry intervals. The first report was that of [Plotnick et al. \(2008, 2009\)](#) of conifer foliar remains in mudstone preserved in sink holes at the northern edge of the basin. This material has been dated as of probable mid-Middle Pennsylvanian (Atokan) age. The conifers appear to have been growing on a limestone karst surface (where were the *Lesleya* and *Megalopteris*, one might ask). The other discovery is from the late-Middle Pennsylvanian (Desmoinesian) ([Falcon-Lang et al., 2009](#)), in the basal gravel lag of a shallow valley fill, laterally equivalent to a calcic Vertisol, thus indicative of a seasonal moisture regime. The paleosol lies immediately beneath the Baker coal bed in western Indiana. Other elements of this flora include cordaitaleans, pteridosperms, and possibly marattialean ferns. Each of these discoveries provides direct proof that conifers and associated xeromorphic floras were present in Middle Pennsylvanian “coal basins” at least during some intervals of time. The physical settings from which they are known all point to periods of periodic moisture limitation in seasonally-dry climates. In addition, the Illinois Basin was not proximate to any upland areas at the time, which might have served as source areas for long-distance transport of this material.

4.2.3.2. Late Pennsylvanian interval. The evidence for parautochthonous conifers and associated drought-tolerant floras is significantly greater during the Late Pennsylvanian than in the Middle Pennsylvanian. In Late Pennsylvanian lowland basins containing coal beds, there are a considerable number of well characterized assemblages dominated by or rich in drought-tolerant plants. These floras are particularly prominent in the early Late Pennsylvanian (Missourian), a time during which the wet–dry climatic spectrum appears to have been broader than that of either the late Middle Pennsylvanian or the late Late Pennsylvanian (Virgilian), based on the morphology and geochemistry of paleosols and the predominant intra-coal-bed sedimentary architectures ([Cecil, 1990](#); [Feldman et al., 2005](#)). However, drought-tolerant floras are present throughout the entire Late Pennsylvanian.

Significant examples of parautochthonous floras containing these xeromorphic elements include the Garnett flora from Kansas ([Cridland and Morris, 1963](#); [Remy et al., 1980](#); [Winston, 1983](#); [Feldman et al., 2005](#)) and the 7–11 flora from Ohio ([McComas, 1988](#); [Wagner and Lyons, 1997](#)). Each of these floras occurs in channel-form deposits between coal beds, not in roof shales, and also in association with vertebrate or invertebrate faunas that also are distinct from wetland faunal assemblages ([Reisz et al., 1982](#); [McComas and Mapes, 1988](#)). They occur within the early Late Pennsylvanian, although not at the immediate Middle–Late Pennsylvanian boundary, thus sometime after the disappearance of most of the arborescent lepidodendrid lycopsids from the western parts of Pangaea. This was the time of maximum climatic drying in the Late Pennsylvanian ([White, 1913b](#); [Cecil et al., 1985](#); [Cecil, 1990](#)). The floras are almost always mixed, including tree ferns and pteridosperms, some of which are also found in wetland assemblages. However, they contain such elements as *Walchia*, *Taeniopteris*, *Plagiozamites*, and *Dichophyllum* and other callipterids. These taxa are consistent components of the more xeromorphic fraction of these floras and, as noted by [Wagner and Lyons \(1997\)](#), occur well into the Permian-age Rotliegendes of Europe ([Kerp and Fichter, 1985](#); [Šimůnek and Martínek, 2009](#)) and the mid-Early Permian of the southwestern United States ([Mamay, 1968](#)). Conifers also have been reported from early Late Pennsylvanian-age rocks of the Conemaugh Formation of the Appalachian Basin, although as isolated reports, not as part of comprehensively described floras ([Darrah, 1975](#); [Lyons and Darrah, 1989](#)).

Conifers and/or other xeromorphic plants, such as callipterid peltasperms, similar to those from the early Late Pennsylvanian, also have been reported in non-roof-shale positions in late Late Pennsylvanian coal-bearing sequences. These include the Baldwin flora ([Cridland and Morris, 1963](#)), Hamilton Quarry flora ([Rothwell and Mapes, 1988](#)), the Calhoun Shale and Topeka Limestone ([Remy et al., 1980](#)), and the Lawrence Shale ([Feldman et al., 2005](#)), all from Kansas, and several floras from Texas ([DiMichele et al., 2005](#)). Most of these occurrences are preserved within channel-fill deposits in shallow incised valleys. In Texas, the floras occur in distinctive kaolinite-rich layers at the base of channel deposits, sometimes eroded into paleosols and often immediately beneath organic shales/coal, from which they appear to be environmentally distinct. The Texas conifer-bearing floras, which are of late Late Pennsylvanian age, very near the Permian boundary, are mainly seed-plant dominated and have few taxa in common with the typical wetland floras that are found in the organic shales/coal and the clastic rocks above them, all occurring in the same outcrops. A varied flora has been reported from the marine Finis Shale in Texas (e.g., [Rothwell et al., 1996](#); [Dunn et al., 2002](#), and other references in those papers) that appears to represent plants not typically found in wetland assemblages, including voynavskyalean conifers, a group known primarily from the north-temperate Angaran floral realm ([Meyen, 1988](#)). Such marine deposits would have formed at times of high sea level, and appear to be associated with seasonally-dry climates.

Conifers in “roof shale” deposits above coal beds are reported from a number of early Late Pennsylvanian coals in the Appalachian region ([McComas, 1988](#); [Blake et al., 1999](#)) and the Western Interior region of the U.S. mid-continent ([DiMichele and Aronson, 1992](#)), but not in the Illinois Basin. Walchian conifers and other plants, such as *Plagiozamites* and *Autunia conferta*, are reported from roof shales of late Late Pennsylvanian and possibly earliest Permian coals in the Appalachians ([Darrah, 1975](#); [Blake et al., 1999](#)). In these instances, the literature rarely is sufficiently detailed to interpret the environmental context of the “roof-shale” deposit, other than to note that it lies immediately superjacent to a coal bed. As [Gastaldo et al. \(1995\)](#) have noted, however, roof shales can represent a wide variety of environments of deposition, many of which are unrelated to the underlying peat/coal bed and do not necessarily represent a drowned final swamp forest.

It is important to note that the occurrence of conifers and associated xeromorphic elements in Late Pennsylvanian deposits does not occur to the exclusion of typically pteridosperm and marattialean-fern dominated floras in the roof shales above most coal beds. In fact, pteridosperm and tree-fern dominated floras are the most characteristic elements of Late Pennsylvanian vegetation to be preserved in all North American and European coal basins. It is particularly important to make note of this for North American deposits (e.g., [Blake et al., 1999](#)). In these rocks, floras containing conifers and other xeromorphic plants have been used to suggest millions of years of missing section. These rare and unusual floras, rich in conifers and other xeromorphic plants, have been characterized as typical of the early Late Pennsylvanian (e.g., [Wagner and Lyons, 1997](#)), which they are not. Also contributing to this missing-time argument are some taxa typical of Late Pennsylvanian (Stephanian late A through C in particular) floras of Europe that are rare or missing in the American sections ([Lyons and Wagner, 1995](#); [Wagner and Lyons, 1997](#)). Missing flora may just as likely be related to latitudinal and longitudinal variation in paleoclimate or to biogeographic factors, as it is to a stratigraphic hiatus. Also, there has been, to date, no demonstration that variation among European floras at this time is any less than between them and eastern North American floras.

As a final point, there are several well documented conifer-dominated floras of early Late Pennsylvanian age from western equatorial Pangaea in sequences completely lacking coal deposits, including the Kinney Quarry ([Mamay and Mapes, 1992](#)) and Carrizo Arroyo ([DiMichele et al., 2004b](#); [Tidwell and Ash, 2004](#)) floras of New

Mexico. In each of these cases, the flora is a mixture rich in a variety of xeromorphic plants, including conifers. These floras are important because they demonstrate that such xeromorphic floras found in basinal lowlands, under climatically seasonal conditions, are fundamentally distinct from the floras of wetlands and the humid climatic conditions that favored peat formation. This helps us to understand that close stratigraphic proximity of humid-climate wetland floras and seasonally-dry floras within coal-bearing cyclic successions is not necessarily evidence of growth in close, laterally continuous spatial association, under a common climate. Rather, it appears that these plants lived under largely different kinds of physical conditions, mainly reflecting climatic differences, as surmised by Elias long ago (1936) (Moore et al., 1936). The intercalation of “wet” and “dry” floras is completely consistent with the fully independent evidence offered by the rocks, including their sedimentology and geochemistry.

5. Discussion

Central to the points raised in this paper is the recognition that plants of any time in geologic history closely reflect climate, if modern times can be taken as a reliable model for the past (Köppen, 1936; Claussen, 1998). Consequently, when autochthonous to parautochthonous floras are found in basinal settings, it is reasonable to presume that those plants grew *in the basins*, rather than that they were transported into the basins from “uplands” (DiMichele et al., 2008). The literature is replete with such interpretations of conifers or cordaitaleans as “upland” plants when found in basinal deposits. In some instances, floral zonation is proposed with the plants assigned *a priori* to elevational zones, even if found co-occurring in parautochthonous deposits. The assumptions in such cases usually are that the lycopsid–sphenopsid–pteridosperm vegetation grew in swamps, the cordaitaleans grew on the margins of the swamps in the low elevations, and the conifers grew yet further up the slopes, the entire matter being controlled by drainage (for a recent example of this kind of *a priori* reasoning see Stephenson et al., 2008). This should not be the default or null model. Such an interpretation stands in competition with the model that all the co-occurring elements could grow in the basinal lowlands in close proximity whenever the necessary soil moisture regimes developed. In this way, the two (or other) interpretations can stand side-by-side and be assessed for relative likelihood through analysis of ancillary data, such as sedimentary environment or climate proxy indicators.

Empirical studies of fossil floras have revealed that more than one kind of flora characterized basinal wetlands, and that those floras were distinct compositionally, with various degrees of overlap. Thus, we must reconsider our image of the Pennsylvanian as a time when coastal lowlands were populated solely by vast wetland swamps, growing in steaming jungles. The lowlands may have been the province of seasonally-dry climates, and the plants that characterize those climates, for as much or more time as the wetlands were dominant.

If this is correct, a question arises of why floras of seasonally-dry habitats are so poorly represented in basinal lowland deposits? This occurs even though these lowlands were subject to extended periods of subhumid to semi-arid climates, over periods of tens of thousands of years, based on sedimentological and paleosol evidence (e.g., Driese and Ober, 2005; Feldman et al., 2005)? Perhaps depocenters in lakes or abandoned channels were sufficiently sparse or were positioned on the terrestrial landscape at sufficient elevations above sea level to be unlikely to be preserved. Preservation of suitable depocenters requires both rapid aggradation and high water table for preservation. Dry-lands, in contrast to this, are deflationary and have a subdued water table, something especially to be expected if these floras were most common during times of dropping sea level and valley incision during glacial phases. In this situation, plants would only have been preserved when they fell into holes that were below the water table and also aggrading (incised valley fills or lakes). Environments such as

the Lower and Middle Pennsylvanian sinkholes reported by Leary (Leary and Pfefferkorn, 1977; Leary, 1981) and Plotnick et al. (2009) are notable examples. Additionally, there is the matter of “search image.” Conifer-containing floras, for example, have been reported often in association with the basal fill of channels scoured during sea-level low-stands (Reisz, 1990; Feldman et al., 2005; Falcon-Lang et al., 2009). Such exposures are not only difficult to find (surface coal mines providing perhaps the best opportunities, as the authors can attest to through personal experience), but plant preservation is often poor, not conducive to the kinds of morphological and taxonomic studies that are favored in paleobotany. Thus, we surmise that many of these seasonally-dry floras remain to be found through focused searches in particular facies (e.g., Fielding et al., 2009).

Seasonally-dry vegetation also is not one compositionally uniform thing. There is actualistic and fossil evidence to suggest much variation in dominance and diversity patterns among seasonally-dry floras within basinal lowlands. Seasonal drought accentuates small differences in soil composition, micro-elevation, and exposure, leading to subtle or major variation in habitat quality compared to that apparent on the same landscape under humid or perhumid climates. Such variation probably was present in regions outside of humid/perhumid-climate belts, whether upland (where elevational factors would be accentuated) or basinal. In addition, given that “dry” climates encompass a much wider range of climate variance than humid–perhumid climates, the basinal vegetation of seasonally-dry periods will be much more reflective of local peculiarities in habitat conditions. Furthermore, the small number of examples of such vegetation in the Pennsylvanian, and the restricted geographic areas from which they are known at any given time, limits our understanding of the patterns and the manner in which floristic variation is organized and distributed within those seasonally-dry landscapes.

A final, and important, question to ask, one that derives directly from the recognition that basins spent long periods of time “not wet,” is where did the wetland vegetation go, or what happened to it when these other kinds of floras prevailed in the basinal lowlands? This has received much less consideration than the dynamic history and composition of so-called “upland” floras in the fossil record. Yet, there is a conservatism to these humid/perhumid floras. They disappear and then reappear in abundance in the basinal lowlands at 10^3 to 10^4 times-scales, again and again over periods of millions of years, with little change in composition or in dominance–diversity structure (Knoll, 1985; Phillips et al., 1985; DiMichele et al., 1987, 1996; Pfefferkorn et al., 2000; DiMichele et al., 2002, 2004a). Such wetland floras even persist well into the Permian in the microcontinents of the eastern Tethyan region (Hilton and Cleal, 2007). Yet, what happened to the flora of wetlands, especially peat-forming environments, when the basinal lowlands were dry? Frankly, there is little evidence from which interpretations can be derived. Did these apparently persistent species assemblages, with long lasting dominance–diversity structure, break up into small refugia or did they migrate to the basin margins, or even out of the basins entirely, and exist intact somewhere outside the sampling envelope? Peat swamps may have been environmentally stressful places to live where only a few hardy specialists could survive. If, on the other hand, peat swamps were a good place to live, then when they reappeared after each dry interval, one might expect a free-for-all with taxa that earlier lived outside the swamp occasionally establishing themselves as dominants in these habitats. That is not what we, in general, see. The same suspects return to positions of dominance again and again, suggesting they were the only plants that could do so, at least without major extinction-inducing environmental disruptions. Hence it could be argued that refugia could be quite small (just big enough to maintain diversity). Large populations are not needed to re-establish the coal swamps, because no other taxa were capable of doing so. Refugia might comprise numerous scattered “water holes” across a dry landscape like those described by Falcon-Lang et al. (2004).

Two possibilities to explain this pattern are considered here. (1) If survival were refugial, a dynamic system of assembly and disassembly is implied. Reassembly from refugia could result in recurrent dominance–diversity conditions simply on the basis of the numbers (conservation of relative proportions as populations expanded into renewed favorable landscapes). There is some limited, but nonetheless significant, evidence to support this (Falcon-Lang, 2004b). In addition, occasional major shifts in abundance patterns, such as the major rise of cordaitaleans in peat swamps in the early Middle Pennsylvanian (Phillips and Peppers, 1984) or the progressive rise of tree ferns in the late Middle Pennsylvanian (Pfefferkorn and Thomson, 1982; Phillips et al., 1985), are far more easily accomplished if there is strong selection while such wet floras are confined to much-reduced refugial areas. This may have occurred during times of climatic conditions broadly unfavorable to them. Highly reduced population sizes could permit strong selective effects to be manifested, resulting in the reshuffling of dominance.

(2) If intact persistence-and-migration is the mechanism, a climate model is called for under which large expanses of humid–perhumid conditions existed in the peribasin equatorial tropics or in paratropical regions. At present, there is no evidence to support such a model (Horton et al., 2007; Tabor and Poulsen, 2008). Furthermore, an ecological explanation is needed for the occasional major shifts in dominance–diversity patterns that appear throughout the Pennsylvanian; this is much more difficult to accomplish in intact, widespread vegetation because of strong incumbency effects, unless one invokes periodic catastrophic climate change of short duration that would permit restructuring. We, thus, favor the first, refugial model, as more likely at this time and more in keeping with what we understand of plant evolutionary dynamics and floristic responses to climate change.

Acknowledgements

This paper is dedicated to Professor Hermann Pfefferkorn for his contributions to the understanding of Carboniferous and Permian vegetation, particularly for his unflagging commitment to enlivening it in our imaginations. The senior author, in particular, owes much to Professor Pfefferkorn for his years of advice, guidance, and friendship. This work was supported by grants from the Smithsonian Institution endowment and scholarly studies funds to WD, NSF grant EAR-545654 to IPM, and a NERC Advanced Fellowship held at Royal Holloway to H F-L. We thank Christopher Cleal and Stanislav Opluštil for their constructive reviews of an earlier version of this paper. We also extend our thanks to Mark H. Scheihing and Christopher Wnuk for their encouragement, patience, and editorial improvements to the manuscript.

References

- Anderson, J.A.R., 1964. The structure and development of the peat swamps of Sarawak and Brunei. *Journal of Tropical Geography* 18, 7–16.
- Andrews, E.B., 1875. Description of fossil plants from the coal measures of Ohio. Report of the Geological Survey of Ohio 2 (part 2), 414–426.
- Arnold, C.A., 1934. A preliminary study of the fossil flora of the Michigan Coal Basin. Contributions, Museum of Paleontology, University of Michigan 4, 177–204.
- Arnold, C.A., 1941. Some Paleozoic plants from central Colorado and their stratigraphic significance. University of Michigan, Contributions, Museum of Paleontology 6, 59–70.
- Arnold, C.A., 1949. Fossil plants of the Michigan Coal Basin. Contributions, Museum of Paleontology, University of Michigan 7, 131–269.
- Bartram, K.M., 1987. Lycopod succession in coals: an example from the Low Barnsley Seam (Westphalian B), Yorkshire, England. *Geological Society, London, Special Publications* 32, 187–199.
- Bateman, R.M., 1991. Paleobotany. In: Cleal, C.J. (Ed.), *Plant Fossils in Geological Investigation: The Paleozoic*. Ellis Horwood, Chichester, UK, pp. 34–116.
- Behrensmeyer, A.K., Hook, R.W., 1992. Paleoenvironmental contexts and taphonomic modes. In: Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.D., Wing, S.L. (Eds.), *Evolutionary Paleobiology of Terrestrial Plants and Animals*. University of Chicago Press, Chicago, pp. 15–136.
- Behrensmeyer, A.K., Kidwell, S.M., Gastaldo, R.A., 2000. Taphonomy and paleobiology. *Paleobiology* 26, 103–147.
- Bertier, P., Swennen, R., Lagrou, D., Laenen, B., Kemps, R., 2008. Palaeo-climate controlled diagenesis of the Westphalian C & D fluvial sandstones in the Campine Basin (north-east Belgium). *Sedimentology* 55, 1375–1417.
- Besly, B.M., Fielding, C.R., 1989. Palaeosols in Westphalian coal-bearing and red-bed sequences, central and northern England. *Palaeogeography, Palaeoclimatology, Palaeoecology* 70, 303–330.
- Besly, B.M., Turner, P., 1983. Origin of redbeds in a moist tropical climate (Etruria Formation, Upper Carboniferous, U.K.). In: Wilson, R.C.L. (Ed.), *Residual Deposits: Special Publications of the Geological Society, London*, vol. 11, pp. 131–147.
- Bishop, J.W., Montañez, I.P., Gulbranson, E.L., Brenckle, P.L., 2009. The onset of mid-Carboniferous glacio-eustasy: sedimentologic and diagenetic constraints, Arrow Canyon, Nevada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 276, 217–243.
- Bishop, J.W., Montañez, I.P., Osleger, D.A., 2010. Dynamic Carboniferous climate change, Arrow Canyon, Nevada. *Geosphere* 6, 1–34.
- Blake, B.M., Beuthin, J.D., 2008. Deciphering the mid-Carboniferous eustatic event in the central Appalachian foreland basin, southern West Virginia, USA. In: Fielding, C., Frank, T. (Eds.), *Resolving the Late Paleozoic Ice Age in Time and Space: Geological Society of America Special Paper*, vol. 441, pp. 249–260.
- Blake Jr., B.M., Cross, A.T., Eble, C.F., Gillespie, W.H., Pfefferkorn, H.W., 1999. Selected plant megafossils from the Carboniferous of the Appalachian Region, Eastern United States: geographic and stratigraphic distribution. In: Hillis, L.V., Henderson, C.M., Bamber, E.W. (Eds.), *Carboniferous and Permian of the World: Canadian Society of Petroleum Geologists Memoir*, vol. 19, pp. 259–335.
- Broutin, J., Doubinger, J., Langiaux, J., Primey, D., 1986. Conséquences de la coexistence de flores à caractères stéphanien et autunien dans les bassins limniques d'Europe occidentale. *Mémoires Société Géologique France NS* 149, 15–25.
- Broutin, J., Doubinger, J., Farjanel, G., Freyret, P., Kerp, H., Langiaux, J., Lebreton, M.L., Sebban, S., Satta, S., 1990. Le renouvellement des flores au passage Carbonifère–Permien: approche stratigraphique, biologique, sédimentologique. *Comptes Rendus de l'Académie des sciences Paris II* 311, 1563–1569.
- Burnham, R.J., 1989. Relationships between standing vegetation and leaf litter in a paratropical forest—implications for paleobotany. *Review of Palaeobotany and Palynology* 58, 5–32.
- Burnham, R.J., 1993. Reconstructing richness in the plant fossil record. *Palaios* 8, 376–384.
- Calder, J.H., 1998. The Carboniferous evolution of Nova Scotia. *Geological Society, London, Special Publications* 143, 261–302.
- Canright, J.E., 1959. Fossil plants of Indiana. Indiana Department of Conservation, Geological Survey Report of Investigations 14, 1–45.
- Cecil, C.B., 1990. Paleoclimate controls on stratigraphic repetition of chemical and siliciclastic rocks. *Geology* 18, 533–536.
- Cecil, C.B., 2003. The concept of autocyclic and allocyclic controls on sedimentation and stratigraphy, emphasizing the climatic variable. In: Cecil, C.B., Edgar, T.N. (Eds.), *Climate Controls on Stratigraphy: SEPM Special Publication*, vol. 77, pp. 13–20.
- Cecil, C.B., Dulong, F.T., 2003. Precipitation models for sediment supply in warm climates. In: Cecil, C.B., Edgar, T.N. (Eds.), *Climate Controls on Stratigraphy: SEPM Special Publication*, vol. 77, pp. 21–27.
- Cecil, C.B., Stanton, R.W., Neuzil, S.G., Dulong, F.T., Ruppert, L.F., Pierce, B.S., 1985. Paleoclimate controls on late Paleozoic sedimentation and peat formation in the Central Appalachian Basin (U.S.A.). *International Journal of Coal Geology* 5, 195–230.
- Cecil, C.B., Dulong, F.T., Cobb, J.C., Supardi, 1993. Allogenic and autogenic controls on sedimentation in the central Sumatra basin as an analogue for Pennsylvanian coal-bearing strata in the Appalachian basin. In: Cobb, J.C., Cecil, C.B. (Eds.), *Modern and Ancient Coal-forming Environments: Geological Society of America Special Paper*, vol. 286, pp. 3–22.
- Cecil, C.B., Dulong, F.T., West, R.R., Stamm, R., Wardlaw, B., Edgar, N.T., 2003a. Climate controls on the stratigraphy of a Middle Pennsylvanian cyclothem in North America. In: Cecil, C.B., Edgar, T.N. (Eds.), *Climate Controls on Stratigraphy: SEPM Special Publication*, vol. 77, pp. 151–182.
- Cecil, C.B., Dulong, F.T., Harris, R.A., Cobb, J.C., Gluskoter, H.G., Nugroho, H., 2003b. Observations on climate and sediment discharge in selected tropical rivers, Indonesia. In: Cecil, C.B., Edgar, T.N. (Eds.), *Climate Controls on Stratigraphy: SEPM Special Publication*, vol. 77, pp. 29–50.
- Chaloner, W.G., 1958. A Carboniferous upland flora. *Geological Magazine* 95, 261–262.
- Claussen, M.C., 1998. On multiple solutions of the atmosphere–vegetation system in present-day climate. *Global Change Biology* 4, 549–599.
- Cleal, C.J., Thomas, B.A., 2004. Late Carboniferous palaeobotany of the upper Bideford Formation, north Devon: a coastal setting for a Coal Measures flora. *Proceedings of the Geologists Association* 115, 267–281.
- Costanza, S.H., 1985. *Pennsylvanianoxylon* of Middle and Upper Pennsylvanian coals of the Illinois Basin and its comparison with *Mesoxylon*. *Palaeontographica B* 197, 81–121.
- Cridland, A.A., 1964. *Amyelon* in American coal balls. *Palaeontology* 7, 189–209.
- Cridland, A.A., Morris, J.E., 1963. *Taeniopteris*, *Walchia* and *Dichophyllum* in the Pennsylvanian of Kansas. *University of Kansas Science Bulletin* 44, 71–85.
- Cross, A.T., 1962. The Rushville (Ohio) Pennsylvanian flora. *American Journal of Botany* 49 (6, Part 2 — Abstracts), 669.
- Darrah, W.C., 1975. Historical aspects of the Permian flora of Fontaine and White. In: Barlow, J.A. (Ed.), *West Virginia Geological and Economic Survey, Morgantown, WV*, pp. 81–101.
- Dawson, J.W., 1851. Notice of the occurrence of upright *Calamites* near Pitcou, Nova Scotia. *Journal of the Geological Society, London* 7, 194–196.
- DiMichele, W.A., Aronson, R.B., 1992. The Pennsylvanian–Permian vegetational transition: a terrestrial analogue to the onshore–offshore hypothesis. *Evolution* 46, 807–824.

- DiMichele, W.A., Phillips, T.L., Olmstead, R.G., 1987. Opportunistic evolution: abiotic environmental stress and the fossil record of plants. *Review of Palaeobotany and Palynology* 50, 151–178.
- DiMichele, W.A., Pfefferkorn, H.W., Phillips, T.L., 1996. Persistence of Late Carboniferous tropical vegetation during glacially driven climatic and sea-level fluctuations. *Palaeogeography, Palaeoclimatology, Palaeoecology* 125, 105–128.
- DiMichele, W.A., Stein, W.E., Bateman, R.M., 2001. Ecological sorting during the Paleozoic radiation of vascular plant classes. In: Allmon, W.D., Bottjer, D.J. (Eds.), *Evolutionary Paleocology*. Columbia University Press, New York, pp. 285–335.
- DiMichele, W.A., Phillips, T.L., Nelson, W.J., 2002. Place vs. time and vegetational persistence: a comparison of four tropical mires from the Illinois Basin during the height of the Pennsylvanian ice age. *International Journal of Coal Geology* 50, 43–72.
- DiMichele, W.A., Behrensmeier, A.K., Olszewski, T.D., Labandeira, C.C., Pandolfi, J.M., Wing, S.L., Bobe, R., 2004a. Long-term stasis in ecological assemblages: evidence from the fossil record. *Annual Review of Ecology, Evolution, and Systematics* 35, 285–322.
- DiMichele, W.A., Kerp, H., Chaney, D.S., 2004b. Tropical floras of the Late Pennsylvanian–Early Permian transition: Carrizo Arroyo in context. In: Lucas, S.G., Zeigler, K.E. (Eds.), *Carboniferous–Permian Transition at Carrizo Arroyo*, Central New Mexico: New Mexico Museum of Natural History and Science Bulletin, vol. 25, pp. 105–110.
- DiMichele, W.A., Tabor, N.J., Chaney, D.S., 2005. Outcrop-scale environmental heterogeneity and vegetational complexity in the Permo–Carboniferous Markley Formation of North Central Texas. In: Lucas, S.G., Zeigler, K.E. (Eds.), *The Nonmarine Permian: New Mexico Museum of Natural History and Science Bulletin*, vol. 30, pp. 60–66.
- DiMichele, W.A., Falcon-Lang, H.J., Nelson, W.J., Elrick, S.D., Ames, P.R., 2007. Ecological gradients within a Middle Pennsylvanian peat mire forest. *Geology* 35, 415–418.
- DiMichele, W.A., Kerp, H., Tabor, N.J., Looy, C.V., 2008. Revisiting the so-called “Paleophytic–Mesophytic” transition in equatorial Pangea: vegetational integrity and climatic tracking. *Palaeogeography, Palaeoclimatology, Palaeoecology* 268, 152–163.
- Dimitrova, T.K., Cleal, C.J., 2007. Palynological evidence for late Westphalian–early Stephanian vegetation change in the Dobrudzha Coalfield, NE Bulgaria. *Geological Magazine* 144, 513–524.
- Driesse, S.G., Ober, E.G., 2005. Paleopedologic and paleohydrologic records of precipitation seasonality from early Pennsylvanian “underclay” paleosols, USA. *Journal of Sedimentary Research* 75, 997–1010.
- Dunn, M.T., Mapes, G., Rothwell, G.W., 2002. On Paleozoic plants from marine strata: *Hexaloba finisensia* new genus and species, a trigonocarpalean ovule from the Virgilian (Upper Pennsylvanian: Gzhelian) Finis Shale of Texas. *Journal of Paleontology* 76, 173–180.
- Eble, C.F., 2002. Palynology of late Middle Pennsylvanian coal beds in the Appalachian Basin. *International Journal of Coal Geology* 50, 73–88.
- Eble, C.F., Grady, W.C., 1990. Paleocological interpretation of a Middle Pennsylvanian coal bed in the central Appalachian basin, USA. *International Journal of Coal Geology* 16, 255–286.
- Edgar, N.T., Cecil, C.B., Mattick, R.E., Chivas, A.R., De Deckker, P., Djajidhardja, Y., 2003. A modern analogue for tectonic, eustatic, and climatic processes in cratonic basins: Gulf of Carpentaria, Northern Australia. In: Cecil, C.B., Edgar, T.N. (Eds.), *Climate Controls on Stratigraphy: SEPM Special Publication*, vol. 77, pp. 193–205.
- Eggert, D.A., 1972. Petrified *Stigmara* of sigillarian origin from North America. *Review of Palaeobotany and Palynology* 14, 85–99.
- Ehret, D.L., Phillips, T.L., 1977. *Psaronius* root systems—morphology and development. *Palaeontographica* B161, 147–164.
- Elias, M.K., 1936. Late Paleozoic Plants of the Midcontinent Region as Indicators of time and Environment. 16th International Carboniferous Congress Report, vol. 1, pp. 691–700.
- Falcon-Lang, H.J., 2003a. Response of Late Carboniferous tropical vegetation to transgressive–regressive rhythms at Joggins, Nova Scotia. *Journal of the Geological Society* 160, 643–648.
- Falcon-Lang, H.J., 2003b. Late Carboniferous tropical dryland vegetation in an alluvial-plain setting, Joggins, Nova Scotia, Canada. *Palaios* 18, 197–211.
- Falcon-Lang, H.J., 2003c. Anatomically preserved cordaitalean trees from a dryland alluvial plain setting, Joggins, Nova Scotia. *Atlantic Geology* 39, 259–265.
- Falcon-Lang, H.J., 2004a. Pennsylvanian tropical rain forests responded to glacial–interglacial rhythms. *Geology* 32, 689–692.
- Falcon-Lang, H.J., 2004b. Pennsylvanian upland vegetation and its implications for the demise of the coal-forming tropical biome. *Geologica Balcanica* 34, 39–45.
- Falcon-Lang, H.W., 2005. Small cordaitaleans trees in a marine-influenced coastal habitat in the Pennsylvanian Joggins Formation, Nova Scotia. *Journal of the Geological Society, London* 162, 485–500.
- Falcon-Lang, H.J., 2006. Latest Mid-Pennsylvanian tree–fern forests in retrograding coastal plain deposits, Sydney Mines Formation, Nova Scotia, Canada. *Journal of the Geological Society* 163, 81–93.
- Falcon-Lang, H.J., 2007. A *Cordaixylon* axis from well-drained alluvial plain facies in the Lower Pennsylvanian Joggins Formation of Nova Scotia. *Atlantic Geology* 43, 87–90.
- Falcon-Lang, H.J., Bashforth, A.R., 2004. Pennsylvanian uplands were forested by giant cordaitalean trees. *Geology* 32, 417–420.
- Falcon-Lang, H.J., Bashforth, A.R., 2005. Morphology, anatomy, and upland ecology of large cordaitalean trees from the Middle Pennsylvanian of Newfoundland. *Review of Palaeobotany and Palynology* 135, 223–243.
- Falcon-Lang, H.J., Miller, R.F., 2007. Palaeoenvironments and palaeoecology of the Early Pennsylvanian Lancaster Formation (“Fern Ledges”) of Saint John, New Brunswick, Canada. *Journal of the Geological Society, London* 164, 945–957.
- Falcon-Lang, H.J., Rygel, M.C., Calder, J.H., Gibling, M.R., 2004. An early Pennsylvanian waterhole deposit and its fossil biota in a dryland alluvial plain setting, Joggins, Nova Scotia. *Journal of the Geological Society* 161, 209–222.
- Falcon-Lang, H.J., Benton, M.J., Braddy, S.J., Davies, S.J., 2006. The Pennsylvanian tropical biome reconstructed from the Joggins Formation of Canada. *Journal of the Geological Society, London* 163, 561–576.
- Falcon-Lang, H.J., Nelson, W.J., Elrick, S., Looy, C.V., Ames, P.R., DiMichele, W.A., 2009. Incised channel fills containing conifers indicate that seasonally dry vegetation dominated Pennsylvanian tropical lowlands. *Geology* 37, 923–926.
- Farley, M.B., 1988. Environmental variation, palynofloras, and paleoecological interpretation. In: DiMichele, W.A., Wing, S.L. (Eds.), *Methods and Applications of Plant Paleocology: Paleontological Society, Special Publication*, vol. 3, pp. 126–146.
- Feldman, H.R., Franseen, E.K., Joeckel, R.M., Heckel, P.H., 2005. Impact of longer-term modest climate shifts on architecture of high-frequency sequences (cyclothem), Pennsylvanian of Midcontinent, U.S.A. *Journal of Sedimentary Research* 75, 350–368.
- Ferguson, D.K., 2005. Plant taphonomy: ruminations on the past, the present, and the future. *Palaios* 20, 418–428.
- Fielding, C.R., Frank, T.D., Birgenheier, L., Rygel, M.C., Jones, A.T., Roberts, J., 2008. Stratigraphic imprint of the Late Palaeozoic Ice Age in eastern Australia: a record of alternating glacial and nonglacial climate regime. *Journal of the Geological Society* 165, 129–140.
- Fielding, C.R., Allen, J.P., Alexander, J., Gibling, M.R., 2009. Facies model for fluvial systems in the seasonal tropics and subtropics. *Geology* 37, 623–626.
- Frakes, L.A., Francis, J.E., Syktus, J.I., 1992. *Climate Modes of the Phanerozoic*. Cambridge University Press, Cambridge, UK.
- Frankenburg, J.M., Eggert, D.A., 1969. Petrified *Stigmara* from North America: Part I. *Stigmara ficoides*, the underground portions of Lepidodendraceae. *Palaeontographica* B128, 1–47.
- Galtier, J., Scott, A.C., Powell, J.H., Glover, B.W., Waters, C.N., 1992. Anatomically preserved conifer-like stems from the Upper Carboniferous of England. *Proceedings of the Royal Society of London*, B 247, 211–214.
- Gastaldo, R.A., 1996. Flöznahe and Flözfern assemblages: Potential Predictors of Late Carboniferous Biome Replacement. In: Leary, R.L. (Ed.), *Patterns in Paleobotany: Proceedings of a Czech–U.S. Carboniferous Paleobotany Workshop: Illinois State Museum Scientific Papers*, vol. 26, pp. 19–27.
- Gastaldo, R.A., Degges, C.W., 2007. Sedimentology and paleontology of a Carboniferous log jam. *International Journal of Coal Geology* 69, 103–118.
- Gastaldo, R.A., Huc, A.Y., 1992. Sediment facies, depositional environments, and distribution of phytoclasts in the Recent Mahakam River delta, Kalimantan, Indonesia. *Palaios* 7, 574–591.
- Gastaldo, R.A., Douglass, D.P., McCarroll, S.M., 1987. Origin, characteristics and provenance of plant macrodetritus in a Holocene crevasse splay, Mobile delta, Alabama. *Palaios* 2, 229–240.
- Gastaldo, R.A., Allen, G.P., Huc, A.Y., 1993. Detrital peat formation in the tropical Mahakam River delta, Kalimantan, eastern Borneo: Formation, plant composition, and geochemistry. In: Cobb, J.C., Cecil, C.B. (Eds.), *Modern and Ancient Coal-forming Environments: Geological Society of America Special Paper*, vol. 286, pp. 107–118.
- Gastaldo, R.A., Pfefferkorn, H.W., DiMichele, W.A., 1995. Characteristics and Classification of Carboniferous Roof Shale Floras. In: Lyons, P.C., Morey, E.D., Wagner, R.H. (Eds.), *Historical Perspectives of Early Twentieth Century Carboniferous Paleobotany in North America: Geological Society of America Memoir*, vol. 185, pp. 341–352.
- Gastaldo, R.A., Walther, H., Rabold, J., Ferguson, D., 1996. Criteria to distinguish parautochthonous leaves in Cenophytic alluvial channel-fills. *Review of Palaeobotany and Palynology* 91, 1–21.
- Gastaldo, R.A., Stevanovic-Walls, I., Ware, W.N., Greb, S.F., 2004. Community heterogeneity of Early Pennsylvanian peat mires. *Geology* 32, 693–696.
- Gastaldo, R.A., Pukynova, E., Šimunek, Z., Schmitz, M.D., 2009. Ecological persistence in the Late Mississippian (Serpukhovian, Namurian A) megafloreal record of the Upper Silesian Basin, Czech Republic. *Palaios* 24, 336–350.
- González, C.R., 1990. Development of the Late Paleozoic glaciations of the South American Gondwana in western Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 79, 275–287.
- Greb, S.F., Andrews, W.M., Eble, C.F., DiMichele, W., Cecil, C.B., Hower, J.C., 2003. Desmoinesian coal beds of the Eastern Interior and surrounding basins: the largest tropical peat mires in earth history. In: Chan, M.A., Archer, A.W. (Eds.), *Extreme Depositional Environments: Mega-end members in Geologic Time: Geological Society of America Special Publication*, vol. 370, pp. 127–150.
- Greenwood, D.R., 1991. The Taphonomy of Plant Macrofossils. In: Donovan, S.K. (Ed.), *The Processes of Fossilization*. Belhaven Press, London, pp. 141–169. Ch. 7.
- Gulbranson, E.L., Montañez, I.P., Schmitz, M.D., Limarino, C.O., Isbell, J.L., Marensi, S., Crowley, J.L., in press. High-resolution U–Pb calibration of Carboniferous glaciogenic deposits, Río Blanco and Paganzo basins, Northwest Argentina. *Geological Society of America Bulletin*.
- Haq, B.U., Schutter, S.R., 2008. A chronology of Paleozoic sea-level changes. *Science* 322, 64–68.
- Havlena, V.A., 1961. Die flöznahe und flözferne flor des oberschlesischen Namurs A und B. *Palaeontographica* B180, 22–38.
- Havlena, V.A., 1971. Die zeitgleichen Floren des europäischen Oberkarbons und die mesophyle Flora des Ostrau-Karwiner Stinkohlenreviers. *Review of Palaeobotany and Palynology* 12, 245–270.
- Heckel, P.H., 1986. Sea-level curve for Pennsylvanian eustatic marine transgressive–regressive depositional cycles along midcontinent outcrop belt, North America. *Geology* 14, 330–334.
- Heckel, P.H., 2008. Pennsylvanian cyclothem in Midcontinent North America as far-field effects of waxing and waning of Gondwana ice sheets. In: Fielding, C.R., Frank, T.D., Isbell, J.L. (Eds.), *Resolving the late Paleozoic Ice Age in Time and Space: Geological Society of America Special Paper*, vol. 441, pp. 275–289.

- Heckel, P.H., Gibling, M.R., King, N.R., 1998. Stratigraphic model for glacial-eustatic Pennsylvanian cyclothems in highstand nearshore detrital regimes. *Journal of Geology* 106, 373–383.
- Hernandez-Castillo, G.R., Rothwell, G.W., Mapes, G., 2001. Thucydiaeae Fam. nov., with a review and reevaluation of Paleozoic Walchian Conifers. *International Journal of Plant Sciences* 162, 1155–1185.
- Herrick, C.L., 1904. A coal-measure forest near Socorro, New Mexico. *Journal of Geology* 12, 237–251.
- Hill, R.S., 1981. Consequences of long-distance dispersal of plant macrofossils. *New Zealand Journal of Botany* 19, 241–242.
- Hilton, J., Bateman, R.M., 2006. Pteridosperms are the backbone of seed-plant phylogeny. *Journal of the Torrey Botanical Society* 133, 119–168.
- Hilton, J., Cleal, C.J., 2007. The relationship between Euramerican and Cathaysian tropical floras in the Late Palaeozoic: palaeobiogeographical and palaeogeographical implications. *Earth-Science Reviews* 85, 85–116.
- Holdridge, L.R., 1967. *Life Zone Ecology*, Revised Edition. Tropical Science Center, San José, Costa Rica.
- Hooker, J.D., Binney, E.W., 1855. On the structure of certain limestone nodules enclosed in seams of bituminous coal, with a description of some trigonocarbons contained in them. *Philosophical Transactions of the Royal Society of London* 145, 149–156.
- Horton, D.E., Poulsen, C.J., Pollard, D., 2007. Orbital and CO₂ forcing of Late Paleozoic continental ice sheets. *Geophysical Research Letters* 34, L19708.
- Hower, J.C., Eble, C.F., 2004. Coal facies studies in the eastern United States. *International Journal of Coal Geology* 58, 3–22.
- Isbell, J.L., Lenaker, P.A., Askin, R.A., Miller, M.F., Babcock, L.E., 2003a. Reevaluation of the timing and extent of late Paleozoic glaciation in Gondwana: role of the transantarctic mountains. *Geology* 31, 977–980.
- Isbell, J.L., Miller, M.F., Wolfe, K.L., Lenaker, P.A., 2003b. Timing of late Paleozoic glaciation in Gondwana: was glaciation responsible for the development of Northern Hemisphere cyclothems? In: Chan, M.A., Archer, A.W. (Eds.), *Extreme Depositional Environments: Mega-end Members in Geologic Time*. Geological Society of America, Special Publication, vol. 370, pp. 5–24.
- Isbell, J.L., Koch, Z.J., Szablewski, G.M., Lenaker, P.A., 2008a. Permian glacial deposits in the Transantarctic Mountains, Antarctica. In: Fielding, C.R., Frank, T.D., Isbell, J.L. (Eds.), *Resolving the Late Paleozoic Ice Age in Time and Space*. Geological Society of America Special Publication, vol. 441, pp. 59–70.
- Isbell, J.L., Cole, D.I., Catuneanu, O., 2008b. Carboniferous–Permian glaciation in the main Karoo Basin, South Africa: stratigraphy, depositional controls, and glacial dynamics. In: Fielding, C.R., Frank, T.D., Isbell, J.L. (Eds.), *Resolving the Late Paleozoic Ice Age in Time and Space*. Geological Society of America Special Publication, vol. 441, pp. 71–82.
- Joekel, R.M., 1989. Geomorphology of a Pennsylvanian land surface: pedogenesis in the Rock Lake Shale Member, southeastern Nebraska. *Journal of Sedimentary Petrology* 59, 469–481.
- Joekel, R.M., 1994. Virgilian (Upper Pennsylvanian) paleosols in the Upper Lawrence Formation (Douglas Group) and in the Snyderville Shale Member (Oread Formation, Shawnee Group) of the northern Midcontinent, USA: pedologic contrasts in a cyclothem sequence. *Journal of Sedimentary Research* A64, 853–866.
- Joekel, R.M., 1995. Paleosols below the Ames Marine Unit (Upper Pennsylvanian, Conemaugh Group) in the Appalachian Basin, U.S.A.: variability on an ancient depositional landscape. *Journal of Sedimentary Research* A65, 393–407.
- Kerp, H., Fichter, J., 1985. Die Macrofloren des saarpfälzischen Rotliegenden (?Ober-Karbon – Unter-Perm; SW-Deutschland). *Mainzer Geowissenschaftliche Mitteilungen* 14, 159–286.
- Knoll, A.H., 1985. Exceptional Preservation of Photosynthetic Organisms in Silicified Carbonates and Silicified Peats. *Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences* 311, 111–122.
- Köppen, W., 1936. Das Geographische System der Klimate. In: Köppen, W., Geiger, R. (Eds.), *Handbuch der Klimatologie*, vol. 1, Part C. Gebrüder Borntraeger, Berlin, pp. 1–46.
- Langenheim Jr., R.L., Nelson, W.J., 1992. The cyclothem concept in the Illinois Basin: a review. *Geological Society of America Memoir* 180, 55–72.
- Leary, R.L., 1981. Early Pennsylvanian geology and paleobotany of the Rock Island County, Illinois, area. Part 1: Geology. *Illinois State Museum Reports of Investigations* 37, 1–88.
- Leary, R.L., 1990. Possible Early Pennsylvanian ancestor of the Cycadales. *Science* 249, 1152–1154.
- Leary, R.L., Pfefferkorn, H.W., 1977. An Early Pennsylvanian flora with *Megalopteris* and *Noeggerathiales* from west-central Illinois. *Illinois State Geological Survey Circular* 500, 1–77.
- Lesquereux, L., 1884. Descriptions of the coal flora of the Carboniferous formations in Pennsylvania and throughout the United States. 2nd Pennsylvania Geological Survey, Report of Progress, pp. 695–977.
- Leveridge, B., Hartley, A.J., 2006. The Variscan Orogeny: the development and deformation of Devonian/Carboniferous basins in SW England and South Wales. In: Brechley, P.J., Rawson, P.F. (Eds.), *The Geology of England and Wales*. Geological Society of London, pp. 225–255.
- Libertín, M., Dašková, J., Opluštil, S., Bek, J., Endress, N., 2009. A palaeoecological model for a vegetated early Westphalian intramontane valley (Intra-Sudetic Basin, Czech Republic). *Review of Palaeobotany and Palynology* 155, 175–203.
- Lyons, P.C., Darrah, W.C., 1989. Earliest conifers in North America: upland and/or palaeoecological indicators? *Palaio* 4, 480–486.
- Lyons, P.C., Wagner, R.H., 1995. The Stephanian of North America: Early 1900's controversies and problems. *Geological Society of America Memoir* 185, 293–314.
- Mamay, S.H., 1968. *Russellites*, new genus, a problematical plant from the Lower Permian of Texas. *United States Geological Survey Professional Paper* 593-I, 11–113.
- Mamay, S.H., Mapes, G., 1992. Early Virgilian plant megafossils from the Kinney Brick Company Quarry, Manzanita Mountains, New Mexico. *New Mexico Bureau of Mines and Mineral Resources Bulletin* 138, 61–85.
- Mapes, G., Gastaldo, R.A., 1986. Upper Paleozoic non-peat-accumulating floras: Broadhead, T.W. (Ed.), *Land Plants — Notes for a Short Course*. University of Tennessee, Department of Geological Sciences. *Studies in Geology* 15, 115–127.
- Mapes, R.H., Mapes, G., 1997. Biotic destruction of terrestrial plant debris in the Late Paleozoic marine environment. *Lethaia* 29, 167–169.
- McCann, T., Pascal, C., Timmerman, M.J., Krzywicz, P., López-Gómez, J., Wetzel, L., Krawczyk, C.M., Rieke, H., Lamarche, J., 2006. Post-Variscan (end Carboniferous–Early Permian) basin evolution in Western and Central Europe. In: Gee, D.G., Stephenson, R.A. (Eds.), *European Lithosphere Dynamics*. Geological Society of London, Memoirs, vol. 32, pp. 355–388.
- McComas, M.A., 1988. Upper Pennsylvanian compression floras of the 7–11 Mine, Columbiana County, northeastern Ohio. *Ohio Journal of Science* 88, 48–52.
- McComas, G.A., Mapes, R.H., 1988. Fauna associated with the Pennsylvanian floral zones of the 7–11 Mine, Columbiana County, Northeastern Ohio. *Ohio Journal of Science* 88, 53–55.
- Meyen, S.V., 1988. Gymnosperms of the Angara flora. In: Beck, C.B. (Ed.), *Origin and Evolution of Gymnosperms*. Columbia University Press, New York, pp. 339–381.
- Montañez, I.P., Tabor, N.J., Niemeier, D., DiMichele, W.A., Frank, T.D., Fielding, C.R., Isbell, J.L., 2007. CO₂-forced climate and vegetation instability during Late Paleozoic deglaciation. *Science* 315, 87–91.
- Moore, R.C., Elias, M.K., Newell, M.D., 1936. A “Permian” flora from the Pennsylvanian rocks of Kansas. *Journal of Geology* 44, 1–31.
- Nordt, L., Orosz, M., Driese, S., Tubbs, J., 2006. Vertisol carbonate properties in relation to mean annual precipitation: implications for paleoprecipitation estimates. *Journal of Geology* 114, 501–510.
- Olzowski, T.D., Patzkowsky, M.E., 2003. From cyclothems to sequences: the record of eustasy and climate on an icehouse epeiric platform (Pennsylvanian–Permian, North American Midcontinent). *Journal of Sedimentary Research* 73, 15–30.
- Opluštil, S., Cleal, C.J., 2007. A comparative analysis of some late Carboniferous basins of Variscan Europe. *Geological Magazine* 144, 417–448.
- Opluštil, S., Pešek, J., 1998. Stratigraphy, palaeoclimatology and palaeogeography of the Late Paleozoic continental deposits in the Czech Republic. In: Crasquin-Soleau, S., Izart, A., Vaslet, D., De Wever, P. (Eds.), *Peri-Tethys: Stratigraphic Correlation 2: Geodiversitas*, vol. 20, pp. 597–619.
- Opluštil, S., Pšenička, J., Libertín, M., Šimůnek, Z., 2007. Vegetation patterns of Westphalian and Lower Stephanian mire assemblages preserved in tuff beds of the continental basins of Czech Republic. *Review of Palaeobotany and Palynology* 143, 107–154.
- Opluštil, S., Pšenička, J., Libertín, M., Bashforth, A.R., Šimůnek, Z., Drábková, J., Dašková, J., 2009. A Middle Pennsylvanian (Bolshevik) peat-forming forest preserved *in situ* in volcanic ash of the Whetstone Horizon in the Radnice Basin, Czech Republic. *Review of Palaeobotany and Palynology* 155, 234–274.
- Peppers, R.A., 1996. Palynological correlation of major Pennsylvanian (Middle and Upper Carboniferous) chronostratigraphic boundaries in the Illinois and other coal basins. *Geological Society of America Memoir* 188, 1–111.
- Peppers, R.A., 1997. Palynology of the Lost Branch Formation of Kansas — new insights on the major floral transition at the Middle–Upper Pennsylvanian boundary. *Review of Palaeobotany and Palynology* 98, 223–246.
- Peyser, C.E., Poulsen, C.J., 2008. Controls on Permo-Carboniferous precipitation over tropical Pangaea: a GCM sensitivity study. *Palaeogeography Palaeoclimatology Palaeoecology* 268, 181–192.
- Pfefferkorn, H.W., 1980. A note on the term “upland flora”. *Review of Palaeobotany and Palynology* 30, 157–158.
- Pfefferkorn, H.W., Wang Jun, 2009. *Stigmariopsis*, *Stigmaria asiatica*, and the survival of the *Sigillaria brardii*–*ichthyolepis* group in the tropics of the late Pennsylvanian and early Permian. *Palaeoworld* 18, 130–135.
- Pfefferkorn, H.W., Thomson, M.C., 1982. Changes in dominance patterns in upper Carboniferous plant-fossil assemblages. *Geology* 10, 641–644.
- Pfefferkorn, H.W., Gastaldo, R.A., DiMichele, W.A., 2000. Ecological Stability during the Late Paleozoic Cold Interval. In: Gastaldo, R.A., DiMichele, W.A. (Eds.), *Terrestrial Ecosystems, A Short Course*. Paleontological Society Papers, vol. 6, pp. 63–78.
- Phillips, T.L., Peppers, R.A., 1984. Changing patterns of Pennsylvanian coal-swamp vegetation and implications of climatic control on coal occurrence. *International Journal of Coal Geology* 3, 205–255.
- Phillips, T.L., Peppers, R.A., DiMichele, W.A., 1985. Stratigraphic and interregional changes in Pennsylvanian coal-swamp vegetation: environmental inferences. *International Journal of Coal Geology* 5, 43–110.
- Plotnick, R.E., Kenig, F., Scott, A., Glasspool, I., 2008. Stop 3: Central Quarry. Exceptionally Well-preserved Paleokarst and Pennsylvanian Cave Fills. In: Curry, B. (Ed.), *Deglacial History and Paleoenvironments of Northern Illinois*. Illinois State Geological Survey Open File Report 2008-1, pp. 79–87.
- Plotnick, R.E., Kenig, F., Scott, A., Glasspool, I., Eble, C.F., Lang, W.J., 2009. Pennsylvanian paleokarst and cave fills from northern Illinois, USA: a window into late Carboniferous environments and landscapes. *Palaio* 24, 627–637.
- Poulsen, C.J., Pollard, D., Montañez, I.P., Rowley, D., 2007. Late Paleozoic tropical climate response to Gondwanan deglaciation. *Geology* 35, 771–774.
- Rast, N., 1984. The Alleghenian orogeny in eastern North America. *Geological Society of London Special Publications* 14, 197–217.
- Raymond, A., 1987. Interpreting ancient swamp communities: can we see the forest in the peat? *Review of Palaeobotany and Palynology* 52, 217–231.
- Raymond, A., 1988. The paleoecology of a coal-ball deposit from the Middle Pennsylvanian of Iowa dominated by cordaitalean gymnosperms. *Review of Palaeobotany and Palynology* 53, 233–250.

- Raymond, A., Phillips, T.L., 1983. Evidence for an Upper Carboniferous mangrove community. In: Teas, H.J. (Ed.), *Biology and Ecology of Mangroves: Tasks for Vegetation Science*, vol. 8, pp. 19–30.
- Raymond, A., Costanza, S.H., Slone, E.D.J., 2001. Was *Cordaitea* a Late Carboniferous mangrove? Geological Society of America, 2001 Annual Meeting, Boston, Massachusetts, U.S.A., Abstracts with Programs, p. 74.
- Read, C.B., Mamay, S.H., 1964. Upper Paleozoic floral zones and floral provinces of the United States. United States Geological Survey Professional Paper 454-K, 1–35.
- Rees, P.M., Ziegler, A.M., Gibbs, M.T., Kutzbach, J.E., Behling, P., Rowley, D.B., 2002. Permian phytogeographic patterns and climate data/model comparisons. *Journal of Geology* 110, 1–31.
- Reisz, R.R., 1990. Geology and Paleontology of the Garnett quarry. In: Cunningham, C.R., Maples, C.G. (Eds.), 1990 Society of Vertebrate Paleontology Upper Paleozoic of Eastern Kansas Guidebook: Kansas Geological Survey Open-file Report, vol. 90-24, pp. 43–48.
- Reisz, R.R., Heatn, M.J., Pynn, B., 1982. Vertebrate fauna of late Pennsylvanian rock lake shale near Garnett, Kansas: Pelycosauria. *Journal of Vertebrate Paleontology* 56, 741–750.
- Remy, W., 1975. The floral changes at the Carboniferous–Permian boundary in Europe and North America. In: Barlow, J.A. (Ed.), *The Age of the Dunkard*, Proceedings of the First I.C. White Memorial Symposium: West Virginia Geologic and Economic Survey, pp. 305–352.
- Remy, W., Remy, R., 1975. *Lesleya weilerbachensis* n. sp. aus dem höheren Westphal C des Saar-Karbons. *Argumenta Palaeobotanica* 4, 1–11.
- Remy, W., Remy, R., Leisman, G.A., Hass, H., 1980. Der nachweis von *Callipteris flabellifera* (Weiss 1879) Zeiller 1898 in Kansas, U.S.A. *Argumenta Palaeobotanica* 6, 1–36.
- Rice, J., Rothwell, G.W., Mapes, G., Mapes, R.H., 1996. *Suavitas imbricata* gen. et sp. nov., an anatomically preserved seed analogue of putative lycophyte affinities from Upper Pennsylvanian marine deposits. *American Journal of Botany* 83, 1083–1090.
- Rothwell, G.W., Mapes, G., 1988. Vegetation of a Paleozoic Conifer Community. In: Mapes, G., Mapes, R.H. (Eds.), *Regional Geology and Paleontology of upper Paleozoic Hamilton Quarry Area in Southeastern Kansas*: Kansas Geological Survey Guidebook, vol. 6, pp. 213–223.
- Rothwell, G.W., Whiteside, K.L., 1974. Rooting structures of the Carboniferous medullosan pteridosperms. *Canadian Journal of Botany* 52, 97–102.
- Rothwell, G.W., Mapes, G., Mapes, R.H., 1996. Anatomically preserved vojnovskyaean seed plants in Upper Pennsylvanian (Stephanian) marine shales of North America. *Journal of Paleontology* 70, 1067–1079.
- Rothwell, G.W., Mapes, G., Mapes, R.H., 1997. Late Paleozoic conifers of North America: structure, diversity and occurrences. *Review of Palaeobotany and Palynology* 95, 95–113.
- Rueger, B.F., 1996. Palynological investigation and discovery of climatically induced depositional cycles in the Paradox Formation (Pennsylvanian: Desmoinesian) of southeastern Utah. U.S. Geological Survey Professional Paper 2000-K, 1–22.
- Rygel, M.C., Fielding, C.R., Frank, T.D., Birgenheier, L.P., 2008. The magnitude of late Paleozoic glacioeustatic fluctuations: a synthesis. *Journal of Sedimentary Research* 78, 500–511.
- Scheiing, M.H., Pfefferkorn, H.W., 1984. The taphonomy of land plants in the Orinoco Delta – a model for the incorporation of plant-parts in clastic sediments of Late Carboniferous age of Euramerica. *Review of Palaeobotany and Palynology* 41, 205–240.
- Schumm, S.A., 1968. Speculations concerning paleohydrologic controls of terrestrial sedimentation. *Geological Society of America, Bulletin* 79, 1558–1573.
- Scott, A.C., 1974. The earliest conifer. *Nature* 251, 707–708.
- Scott, A.C., 1978. Sedimentological and ecological control of Westphalian B plant assemblages from west Yorkshire. *Proceedings Yorkshire Geological Society* 41, 461–508.
- Scott, A.C., Chaloner, W.G., 1983. The earliest fossil conifer from the Westphalian B of Yorkshire. *Proceedings of the Royal Society, London* 200B, 163–182.
- Scott, A.C., Galtier, J., Mapes, R.H., Mapes, G., 1997. Palaeoecological and evolutionary significance of anatomically preserved terrestrial plants in Upper Carboniferous marine goniatite bullions. *Journal of the Geological Society London* 154, 61–68.
- Siever, R., 1951. The Mississippian–Pennsylvanian unconformity in southern Illinois. *American Association of Petroleum Geologists Bulletin* 35, 542–581.
- Šimůnek, Z., 1996. Leaves and cuticles of the genus *Lesleya* Lesquereux from the Czech Republic and from Illinois (U.S.A.). *Illinois State Museum, Scientific Papers* 26, 43–56.
- Šimůnek, Z., 2007. New classification of the genus *Cordaitea* from the Carboniferous and Permian of the Bohemian Massif based on micromorphology of its cuticle. *Acta Musei nationalis, Pragae, Series B, Historia Naturalis* 62, 97–210.
- Šimůnek, Z., 2008. The Asturian and Cantabrian floral assemblages with *Cordaitea* from the Plzeň Basin Czech Republic. *Studia Geologica Polonica* 129, 51–80.
- Šimůnek, Z., Martinek, K., 2009. A study of Late Carboniferous and Early Permian plant assemblages from the Boskovice Basin, Czech Republic. *Review of Palaeobotany and Palynology* 155, 275–307.
- Soil Survey Staff, 1999. *Keys to Soil Taxonomy: A Basic System for Soil Classification for Making and Interpreting Soil Surveys*, 2nd Edition. United States Department of Agriculture, Soil Conservation Service Handbook, vol. 436. Washington, DC.
- Soreghan, G.S., Giles, K.A., 1999. Amplitudes of Late Pennsylvanian glacioeustasy. *Geology* 27, 255–258.
- Spicer, R.A., 1981. The sorting and deposition of allochthonous plant material in a modern environment at Silwood Lake, Silwood Park, Berkshire, England. *United States Geological Survey Professional Paper* 1143, 1–77.
- Stephenson, M.H., Millward, D., Leng, M.J., Vane, C.H., 2008. Palaeoecological and possible evolutionary effects of early Namurian (Serpukhovian, Carboniferous) glacioeustatic cyclicity. *Journal of the Geological Society* 165, 993–1005.
- Stopes, M.C., 1914. The “Fern Ledges” Carboniferous flora of St. John, New Brunswick. *Geological Survey of Canada Memoir* 41, 1–142.
- Stopes, M.C., Watson, D.M.S., 1909. On the present distribution and origin of the calcareous concretions in coal seams known as ‘coal balls’. *Philosophical Transactions of the Royal Society B* 200, 167–218.
- Tabor, N.J., Poulsen, C.J., 2008. Paleoclimate across the Late Pennsylvanian–Early Permian tropical paleolatitudes: a review of climate indicators, their distribution, and relation to paleophysiographic climate factors. *Palaeobiology, Palaeoclimatology, Palaeoecology* 268, 293–310.
- Tidwell, W.D., Ash, S.R., 2004. Synopsis of the flora in the Red Tanks Formation, Carrizo Arroyo, New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 25, 97–103.
- Trivett, M.L., Rothwell, G.W., 1991. Diversity among Paleozoic Cordaitales. *Systematic Botany* 10, 205–223.
- Utting, J., Giles, P.S., 2008. Palynostratigraphy and lithostratigraphy of Carboniferous Upper Codroy Group and Barachois Goup, southwestern Newfoundland. *Canadian Journal of Earth Sciences* 45, 45–67.
- Wagner, R.H., 2005. *Dicranophyllum glabrum* (Dawson) Stopes, an unusual element of lower Westphalian floras in Atlantic Canada. *Revista Espanola de Paleontologia* 20, 7–13.
- Wagner, R.H., Lyons, P.C., 1997. A critical analysis of the higher Pennsylvanian megafloora of the Appalachian region. *Review of Palaeobotany and Palynology* 95, 255–283.
- Walter, H., 1985. *Vegetation of the Earth and Ecological Systems of the Geo-biosphere*, 3rd edition. Springer-Verlag, New York.
- Wanless, H.R., Shepard, F.P., 1936. Sea level and climatic changes related to late Paleozoic cycles. *Geological Society of America Bulletin* 47, 1177–1206.
- Wanless, H.R., Wright, C.R., 1978. Paleoenvironment maps of Pennsylvanian rocks, Illinois basin and northern midcontinent region: Geological Society of America, Map and Chart Series, no. 23.
- Waters, C.N., Davies, S.J., 2006. Carboniferous extensional basins, advancing deltas and coal swamps. In: Brechly, P.J., Rawson, P.F. (Eds.), *The Geology of England and Wales*. The Geological Society, London, pp. 173–224.
- Weller, J.M., 1931. The concept of cyclic sedimentation during the Pennsylvanian Period. *Illinois State Geological Survey Bulletin* 60, 163–177.
- White, D., 1908. Report on fieldwork done in 1907. *Illinois State Geological Survey Bulletin* 8, 268–272.
- White, D., 1913a. The fossil flora of West Virginia. *West Virginia Geological Survey Report* 5, 353–390.
- White, C.D., 1913b. Climates of coal forming periods. In: White, C.D., Theissen, R. (Eds.), *The Origin of Coal*: U.S. Bureau of Mines Bulletin, vol. 38, pp. 68–79.
- Winston, R.B., 1983. A Late Pennsylvanian upland flora in Kansas: systematics and environmental implications. *Review of Palaeobotany and Palynology* 40, 5–31.
- Wolfe, J.A., 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *American Scientist* 66, 694–703.
- Woodward, F.I., Lomas, M.R., Kelly, C.K., 2004. Global climate and the distribution of plant biomes. *Philosophical Transactions of the Royal Society, London B* 359, 1465–1476.
- Zhou, Y.-X., 1994. Earliest pollen-dominated microfloras from the early Late Carboniferous of the Tian Shan Mountains, NW China: their significance for the origin of conifers and palaeophytogeography. *Review of Palaeobotany and Palynology* 81, 193–211.
- Ziegler, A.M., 1990. Phytogeographic patterns and continental configurations during the Permian period. In: McKerrow, W.S., Scotese, C.R. (Eds.), *Paleozoic Paleogeography and Biogeography*: Geological Society of London Memoir, vol. 12, pp. 363–379.